

A new subfamily and genus in Achatinidae (Pulmonata: Sigmurethra)

ALBERT R. MEAD

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

THE NATURAL
HISTORY MUSEUM
15 JUL 1994
PRESENTED
ZOOLOGY LIBRARY

CONTENTS

Synopsis	1
Introduction	1
Methods	3
Abbreviations – Anatomical	3
Achatinidae	3
Key to subfamilies	3
Callistoplepinae – new subfamily	3
Key to genera	4
Genus <i>Callistoplepa</i>	5
Key to species	5
Genus <i>Leptocala</i>	12
Key to species	13
Achatininae	18
Genus <i>Bequaertina</i> – new genus	18
Key to species	22
Radulae and jaws	32
Acknowledgements	35
Acronyms	35
References	36

SYNOPSIS. In the Achatinidae, characteristics of the internal anatomy, particularly those in the reproductive tract, are continuing to show greater dependability in determining phylogenetic affinities than those in the shell, radula or jaw. In 1934, J.C. Bequaert reached the conclusion in the course of his revising the African land snail family Achatinidae, 'that several of the East African *Achatinae* are not separable from the West Africa *Callistoplepae*, at any rate as far as shell characters go'. The present 5-year study of over 500 shell specimens and 50 soft anatomies, involving 11 genus-group and 57 species-group nomina, demonstrates that the 4 anatomically distinct West African species, to which Bequaert referred, are the most primitive in the family. Accordingly, they have been placed in a separate subfamily. Anatomically the 5 contrastingly different East African species were found to be a distinct genus, plesiomorphic to subgenus *Achatina* (*sensu* Bequaert, 1950). Their phylogenetic relationships show a strong correlation with the distributional evidence in 60 recorded localities, which delineates (1) a short north central axis, (2) a central to eastern Africa axis, and (3) a strong north-south axis extending from eastern Africa into southern Africa. This evidence supports the emerging pattern of terrestrial gastropod distribution in Africa. The present project forms the foundation for a revision of the family, currently in progress.

INTRODUCTION

Fifty-seven species-group nomina associated with the achatinid genus *Callistoplepa* have provided the basis for the present 5-year project. The examination of over 500 shell specimens and 50 soft anatomies has revealed the fact that four West African anatomically distinct but related Lower Guinea species, in two genera, constitute a separate, primitive subfamily of the Achatinidae. Anatomical and conchological studies place the five other valid species in a new genus that is distributed in Central, Eastern and Southern Africa.

Taxonomy in the Achatinidae is based both on the shell and on the soft anatomy, particularly that of the basal reproductive tract. The shell is a permanent record that reflects ontogenetically the influence of the environment, whereas the soft anatomy reflects phylogenetically the influence of evolution. The latter, in the short term, is relatively free of substantive changes, being limited to temporary variations that reflect nutritional, developmental or reproductive influence. For example, both immature and seriously malnourished mature specimens have misleadingly attenuated, thin reproductive tracts with greatly limited musculature; but the malnourished specimen can be readily distinguished because it has a much larger reproductive tract

with the rich coloration of the mature specimen. Under suitable conditions, both types of individuals are able to assume the basic genital proportions that are typical of the species. In the long term, the shell reflects and responds to the pressures of selection in a changing or in a new environment. Wholly different molluscan stocks moving into distinct but similar environments may evolve convergently into forms that are so similar that conchologically they cannot reasonably be distinguished or identified without first knowing the locality, e.g. *Achatina* (*Lissachatina*) *craveni* Smith, 1881 and *A. (Achatina) tavaresiana* Morelet, 1866 (Mead, 1992). Although in the long term, the soft anatomy undergoes changes, it revealingly does so within a more restricted, basic, generalized pattern obviously characteristic of the larger group of which it is a related part. At this stage of investigations, these larger groups seem to be taking shape within genera and subgenera (*sensu* Bequaert, 1950).

All these factors have so entered into the present project that nine species, once thought to be congeners on the basis of the great similarity in their familial unique shell characters, are now separated into two subfamilies. The shells are remarkably similar, but the soft anatomies convincingly tell a different story. In essence, in the Achatinidae the soft anatomy reveals dependable, differentiating taxonomic criteria at the species level and above; the shell usually reveals supporting taxonomic criteria at the species level and often convincing criteria at the subspecies level. A more clear concept of subspecies is beginning to emerge in this family: Essentially consistent, usually minor shell differences in the members of an allopatric population that have features in their soft anatomy indistinguishable from those of the nominate subspecies. This is precisely why the erstwhile enigmatic *Leptocala petitia* is shown in the text to be a distinct species rather than a subspecies or a synonym of the conchologically very slightly different *L. mollicella*.

The shells of the nine species in this project have been redescribed in the light of larger series of specimens and more detailed examinations of shell characters than in previous studies. In many full grown specimens, weathering and environmental abrasion have obscured or removed valuable shell characters, particularly in the upper whorls. The emphasis on a comparative examination of juvenile specimens in the present study, therefore, has been especially informative. In fact, it strongly supports the value of the collecting juvenile specimens, along with the larger specimens, whenever they are available. For the same reasons, determining the number of whorls is always an imprecise measurement and thus is recorded here only to the nearest one-quarter whorl. The length of the last whorl (= body whorl) includes the entire whorl and is measured from the base of the aperture to the point on the suture immediately above where the outer lip attaches at the periphery. All shell measurements are carried to the nearest 0.1 mm. For many decades the basic horizontal and vertical sculpture of the achatinid shell has been referred to as 'deccusate'; this has been changed in the present work to the more accurate term 'cancellate'. From the shell dimensions, two important relationships are drawn: 1) between the greatest shell width and the shell length, and 2) between the length of the last whorl and the shell length. These relationships are expressed in percentages rather than in ratios. This emphasizes the measurement being compared rather than the measurement to which it is being compared; that is, in making comparisons, it is easier to comprehend that the last whorl is 87% of the shell length, than the fact that the length

is 1.15 times the length of the last whorl. Aperture width does not include the callus. The descriptive shell terminology is largely based on Cox (1960).

Diligent searching in 49 museums and personal collections, fortunately brought to light an unexpected fair number of alcohol preserved specimens. The museums with the largest and most varied collections of alcohol preserved achatinid specimens are in Tervuren, Stockholm, Berlin, Bruxelles, Paris, Frankfurt and London. But very valuable specimens have been found in museums where there is relatively limited material. It was through the convictions of Edmond Dart-velle of the Muséum National de l'Afrique Centrale (Tervuren) that the wet collection of the museum is unparalleled in quantity and diversity. Because the available material used in the present project is limited, determined efforts were made, after establishing the basic genital pattern, to conserve the remaining specimens for future investigators.

The relationships of the basal genital system show to greater comparative advantage in ventral view. For this reason, the line drawings are similarly oriented in this perspective, with the male conduit to the left and the female conduit to the right, unless otherwise indicated. The individual structures of the conduits are spread apart to show their configuration and minimize obstruction. The drawings are idealized, where possible through multiple specimens, to eliminate irrelevant and misleading features produced in preservation. The origin of the penial retractor is on the male conduit at a point that marks the division between penis and vas deferens. As the retractor anlage reaches apically during development, it usually inserts somewhere on the columellar muscle system, but may insert on the body wall, diaphragm, transverse myoseptum or other sites in the haemocoel (Mead, 1950). The configuration of the developing viscera may predispose the manner of insertion. The not infrequent bifurcate (Fig. 20) and multifurcate penial retractor insertions support the ontogenetic rather than the functional interpretation of these terms. Within a species, the site of insertion may be consistent or variable. There is a fairly strong tendency in this family for the basal penial retractor to proliferate muscle and apparently connective tissue that variously produce adhesions in the several parts of the male conduit. This in turn changes the relationship of these parts, alters the extroversion process, and the configuration of the resultant intromittent organ. This organ is normally composed seriatim, apex to base, of the penis, pilaster (when present), penis sheath, penial atrium and genital atrium externally, and the basal vas deferens, penial retractor, apical vas deferens and ejaculatory duct internally.

Directions of left and right refer to those of the snail. Apical, in reference to the genital system, means toward the ovotestis, basal toward the genital atrium. The anatomical terminology is essentially that of Mead (1950) (see Abbreviations – Anatomical below).

The discussion of each species is in the following format: shell, soft anatomy (where available), type material, type locality, distribution and, when applicable, remarks. The sources and localities of the alcohol-preserved specimens are reported in the text. A table for each species includes the sources of all shell specimens examined, taxonomically important specimens, illustrated specimens, a size range, their localities, shell dimensions and shell proportions. Illustrations in the literature are cited in the synonymies; the nature of the illustration, where it is other than of the shell, is shown in parentheses. Most localities were found in the

volumes of the U.S. Board of Geographic Names and their locality figures were preferentially used. A list of acronyms of institutions and private collections follows the text. Symbols and abbreviations used in the Tables: Holo = Holotype, L = Length, Lect = Lectotype, LW = Last Whorl, Para = Paratype, PLec = Paralectotype, W = greatest Width, † = dissected, * = see photograph.

Continued research along the lines of Mead (1950, 1978, 1992) and in the present work promises to establish a sound taxonomic and phylogenetic base for the Achatinidae.

METHODS

Examining a great number of variously preserved whole specimens in the present project has once again emphasized the importance of using proper preservation procedures. Ideally, specimens selected for preservation of the soft parts should be put in previously boiled water that has reached ambient temperature. They should drown normally 8–12 hours. Overdrowning will cause the basal genital structures to evert, irreparably distorting the taxonomically valuable features. Underdrowning permits the specimen to withdraw excessively into the shell. Crowding the specimens or using too small a volume of fluid promotes maceration. The adequately drowned specimen usually contracts slightly when placed in the initial 40% alcohol. In a few hours, depending upon the size of the specimen, it should next be placed in a 60% solution, followed by at least one change to 70% alcohol.

Formalin is a powerful, penetrating, irritating fixative. If it is used at a very low percentage for a short period before the specimen is washed thoroughly and transferred to 70% alcohol, it can be quite effective. But in general, its use should be avoided because formalin alters the colour of the shell, makes the shell brittle and chalky, causes the periostracum to crack and peel off upon drying, promotes adhesions between the shell and soft parts, severely hardens the muscular body wall, and precipitates great quantities of albumin and recrystallized calcareous islands in the tissues. As a result, extrication rarely can be accomplished without damage to both shell and soft parts. Further, even with prolonged soaking in a 0.5% trisodium phosphate solution, the muscular body wall remains so hard and tough that, with extreme difficulty it has to be snipped out, piece by small piece, to get to the soft parts, which often are so intensely fixed that they are brittle. Once the soft parts are removed, they usually can be relaxed for limited manipulation only by further soaking in trisodium phosphate and one or more prolonged water baths. Even then, a distressing degree of brittleness remains. The practice of 'neutralizing' formalin for the preservation of vertebrate specimens by first dropping live snail specimens in the solution is deplorable.

ABBREVIATIONS – ANATOMICAL

AVD	apical vas deferens
BVD	basal vas deferens
E	egg
EM	eversion muscle bands
FO	free oviduct

GA	genital atrium
OTD	ovotestis duct
P	penis
PA	penial atrium
PIL	pilaster
PR	penial retractor
PS	penis sheath
RCR	right columellar retractor
ROR	right ommatophore retractor
S	spermatheca
SD	spermathecal duct
SO	spermoviduct
SSV	secondary seminal vesicle
T	talon
V	vagina
VA	vaginal atrium
VR	vaginal retentor

Achatinidae

Basal genital conduits simple, without accessory organs. A conspicuous sheath partially, or usually, completely envelops the penis. Spermatophores not formed. The right branch of the columella muscle system regularly remains to the left of the genitalia. Kidney long, two to three times the length of the pericardium; sigmurethrous. Pulmonary vein without major branches. Holopod. Rachidian tooth very slender and apparently nonfunctional, rarely wide. Jaw simple; smooth or usually striated. Shell ovate, elongate-ovate or conic-oblong, rarely columnar; anomphalous or umbilicate; columella truncate or continuous with outer lip, some forms are intermediate. Endemic in continental Africa and its adjacent small coastal islands; four known introduced species elsewhere in the world.

Key to Subfamilies

Vas deferens does not penetrate the penis sheath, but leaves apically with the penial retractor through the sheath aperture. The penial retractor inserts on the right columellar retractor; it is extremely short, entirely or almost entirely covered by the penis sheath; penis contains a large, conspicuous pilaster. Rachidian tooth about as wide as the laterals CALLISTOPLEPINAE

Vas deferens penetrates the penis sheath. Even within a single population, the penial retractor may variously insert on muscle bands, body wall, diaphragm or fascia; it is usually long to very long and entirely or almost entirely free of the penis sheath; penis contains an ill-defined pilaster, no pilaster, or a verge. Rachidian tooth usually much narrower than the laterals ACHATININAE

CALLISTOPLEPINAE – new subfamily

This subfamily contains the most primitive achatinids yet known. Phylogenetically, it is at the base of the Achatinidae, near the Subulinidae. Like that in the Subulinidae, the vas deferens does not penetrate the penial sheath. The more ovate, patterned shell, however, with its larger aperture and limited number of whorls places this taxon in the Achatinidae rather than the Subulinidae. Supportive of this are the long kidney and the pattern of lung venation. The radula is uncharacteristic of either family, but this is of lesser impor-

tance phylogenetically because this structure is well known to be responsive to changing feeding habits within closely related species. The wide, functional rachidian tooth immediately distinguishes the Callistoplepinae from most Achatiniinae (Fig. 58–63). D'Ailly (1896:69) was the first to examine and illustrate the radulae of both species of *Callistoplepa* (see also Pilsbry, 1904:ix,xv; Thiele, 1929:560 and Ortiz & Ortiz, 1959:46). In the present study, the radulae of *C. barriana* (Sowerby, 1890), *C. shuttleworthi* (Pfeiffer, 1856) and *Leptocala mollicella* (Morelet, 1860) were found to follow the same basic form and pattern. Similarly all the jaws are essentially identical – simple, nearly smooth, fulvous, chitinous collariform band that is somewhat wider in the middle and tapering at the sides. There is no suggestion of even generic difference in these structures. Thus, with only two alcohol specimens of *L. petitia* (Jousseaume, 1884) extant, a decision was made to leave their odontophores intact.

All four species in the Callistoplepinae are limited geographically (ca 5° N–5° S) to the tropical Lower Guinea region of West Africa, which at this point appears to be the cradle of the Achatinidae (Mead, 1992). The high natural luster of their translucent, elongate-ovate shells probably reflects selective advantage in the protractedly wet rainforest. Prior to the present study, the soft anatomy had been examined in one or more species in the eleven achatinine genera except the Guinean genus *Columna* (none so far available) and all except four of the thirteen achatinine subgenera (*sensu* Bequaert, 1950). All that have been examined clearly are anatomically more advanced than the two callistoplepine genera.

The calcareous, thick-shelled eggs are comparatively large for the family and are on a par with those of *Tholachatina*. D'Ailly (1896:68) felt they were somewhat small compared to the size of the snail shell. Thiele (1929:560) echoed this point; but d'Ailly apparently was comparing them with the relatively huge eggs of some *Archachatina* and the subulinids. A reticulate-microtuberculate texture covers the slender, attenuated body. Basally, the mantle is generously covered with variable size, fusing black to gray spots; these show through the thin shell. Apically, the spots are smaller, more regular and concentrated on the shoulder of the whorls. The genital orifice appears to be unusually far posterior; Ortiz & Ortiz (1959) made this observation in *C. shuttleworthi*.

Typical of the known achatinids, the anterior aorta in the Callistoplepinae is found on the dorsal surface of the diaphragm where it abruptly penetrates the diaphragm to pass vertically along the anterior edge of the sagittal myoseptum. Anteriorly, this latter separates the right and left columellar retractors and incompletely places the male and female basal conduits in left and right chambers, respectively. In all four species, the triangular kidney is long, 2–3 times the length of the pericardium, and sigmoid. The ascending limb of the urethra is closed for its entire length. Venation of the lung is a dense, broad network on the pericardial side of the slender principal vein, whereas on the right of the principal vein there is a relatively narrow band of parallel, limited branching veins between it and the ascending limb of the ureter. The second largest vein, about half the caliber of the principal vein, starts as a network in the far left posterior corner of the lung, anastomoses, and joins the principal vein at a right angle 5–7 mm anterior to the kidney.

Together, the four included species in this subfamily manifest seriatim, from simple to complex, an impressive transition series in the basal male conduit from what surely is a pilaster to that which appears to be a verge or penis papilla. *Callistoplepa barriana* is the most primitive with an elongate, elevated pilaster on the ventral penial wall. In *C. shuttleworthi* the apical penis has permanently partially evaginated, pulling dorsally the basal-most part of the vas deferens into the pilaster and fixing it in place with tissue derived from the adjacent penial retractor. This progression is taken one step further in *Leptocala petitia*, wherein the permanently evaginated apical penis becomes so greatly enlarged, thick-walled and dorsoventrally distorted that the resultant pilaster essentially fills the thin-walled, saccular basal penis. Finally in *L. mollicella*, the pilaster assumes an apical position wherein it is axially pendulous within the thick-walled basal penis. At first glance, it appears to be a penis papilla, but the asymmetry within betrays the fact that it is in actuality a greatly modified pilaster. In all four species, the penial retractor is extremely short and inserts on the right columellar retractor. In *C. shuttleworthi* it inserts forward near the other branches; in the other species it inserts far to the rear. The penis sheath is so thin that it is difficult to trace; but it naturally enshrouds the entire penis, allowing the penial retractor and the vas deferens to pass out apically through the aperture of the sheath. A barely discernible transparent tissue layer attached directly on the surface of the penis is formed by the penial retractor. This may be the forerunner of the condition found in some Angolan achatinids, e.g. *Achatina welwitschi* Morelet, 1866, in which the penis is buried in dense muscle tissue extending from the penial retractor. Both the inner surface of the penis sheath and the adjacent but continuous outer surface of the penis are smooth, shiny and free from each other. This condition facilitates seriatim extroversion.

The spermatheca is consistently attached to the spermoviduct well above the junction of the apical vas deferens and the free oviduct. In the adult forms, there is no distinct vaginal retentor between the vagina and the body wall. In juvenile specimens of *C. shuttleworthi*, however, the anlage is present, which suggests that in this subfamily, its full development may be obviated by the highly developed, muscular basal female conduit.

Type genus: *Callistoplepa* Ancey, 1888.

Key to Genera

Sculpture of body whorl coarse, with slender, tightly and evenly placed prosocline costate ridges; shell aperture large, usually 52% of shell length; last whorl long, usually > 73% of shell length. Posterior foot with dorsolateral serrate ridges. No colored band on neck. Equatorial Guinea to Nigeria *Callistoplepa*
Sculpture of body whorl with extremely finely engraved microscopic rhomboids or vertical vermiculate granulae; shell aperture modest, usually > 52% of shell length; last whorl shorter, usually > 73% of shell length. Foot without dorsolateral ridges. Dark gray band on neck between ommatophores and mantle. Cameroon to western Zaire *Leptocala*

*Callistoplepa**Callistoplepa*

Ancey, 1888:69 (footnote 2 for '*Achatina shuttleworthiana*' [sic = *A. shuttleworthi* Pfeiffer, 1856]); Pilsbry, 1905:viii, ix (fig. 2), xv (radula); Germain, 1909:90; Pilsbry, 1919:54, 60, 80, fig. 25 (map); Bequaert & Clench, 1934c:114; Ortiz & Ortiz, 1959:44; Zilch, 1959:372; Mead, 1986:144.

Ganomidos

d'Ailly, 1896:66. Type species by present designation, *Achatina barriana* Sowerby, 1890.

Callistoplepa

Ancey, 1898:92 (type species: *Achatina shuttleworthi* Pfeiffer, 1856); Thiele, 1929:560; Germain, 1936:151 (footnote 3); Verdcourt, 1966:111; Meredith, 1983:30; Oliver, 1983:9; Parkinson, *et al.* 1987:68; Vaught, 1988:90.

Ganomides

Boettger, 1905:170.

Ganomides

Verdcourt, 1966:111.

Callistoplepa s.s.

Mead, 1992.

After an extended trip to West Africa, a Captain Vignon prepared a catalogue of 104 land and freshwater molluscs that he had collected. The shells and the catalogue were subsequently acquired by a collector in Marseille and made available to his colleague C.F. Ancey, who was given the opportunity to publish this catalogue. Ancey (1888) agreed to present it 'such as it is, but with necessary, even indispensable, annotations because of defective identifications, some of which are not found to be at the level of the science' (*trans.*). In one of many footnote annotations, he placed '*Achatina shuttleworthiana*' [sic] under a new generic name '*Callistoplepa*'. If Ancey was not responsible for the misspelling of the specific name '*shuttleworthi*', then at least he did not correct it. The greater misfortune was that he misspelled the proposed generic name, which as revealed later (Ancey, 1898) was intended to be '*Callistoplepa*' (Gr. most beautiful robe).

In view of Ancey's casual manner of publishing the description of this genus, the spelling of the generic name '*Callistoplepa*' must be considered to be the 'correct original spelling' (ICZN Art. 32 (b) and is 'to be preserved unaltered'. According to Art. 32 (c), Ancey's name does not qualify as an 'incorrect original spelling' because, 'without recourse to . . . external source of information,' there is no 'clear evidence of an inadvertent error' even though orthographically it would have been desirable to have spelled it '*Callistoplepa*'. His unorthodoxy and failure to make a timely correction in spelling suggested that he was content for ten years to leave it in its original form. In the meantime d'Ailly (1896) unwittingly proposed the generic synonym *Ganomidos* including *Achatina shuttleworthi* along with *A. barriana*. Further, Ancey's original spelling contravenes no provisions of the Code articles. It is only in his belated publication (1898) that he used the spelling '*Callistoplepa*', without even implied justification for the change in spelling. Under the circumstances, this constituted an 'unjustified emendation' of the original spelling and therefore it is a junior objective synonym (Art. 33 (b)(iii)). Or, perhaps it was just another one of his regrettable misspellings. This rationale supports Pilsbry's conclusions (1905:126), but not those of Germain (1936:151

footnote 3). Unfortunately, the confusion about the valid spelling of the generic name has persisted in collections and even in the more recent literature, e.g. Parkinson *et al.*, 1987:68, Vaught, 1988:90. It is hoped that the present explanation finally will obviate any further confusion.

Ancey (1888) gave as the outstanding characteristics of this new genus its totally different appearance, thin shell, fine striation, and a colour pattern recalling *Orthalicus gallinasultana*. d'Ailly (1896) was the first to describe adequately this taxon, emphasizing the delicate, translucent, shiny, white-flecked shell, the vertical filiform sculpture, the mammillate apex, the inflated body whorl, the elongate, serrate-cristate foot, the hard-shelled eggs, and the unusual radulae of both *Ganomidos shuttleworthi* and the then, newly embraced *G. barriana*. Pilsbry (1905) accepted broadly d'Ailly's characterization of the genus and emphasized the importance of the very thin shell, the closely 'ribpligate' sculpture and the broad central tooth of the radula. In addition, he included in Ancey's genus *Callistoplepa*: *Ganomidos pellucidus* Putzeys, 1898, *G. fraterculus* Dupius & Putzeys, 1900, *Achatina marteli* and its subspecies *A. m. pallescens* Dautzenberg, 1901. Germain (1909) and Pilsbry (1919) retained this grouping. Bequaert & Clench (1934c) added to this genus on the basis of shell characters: *Achatina nyikaensis* Pilsbry, 1909 and *A. graueri* Thiele, 1911. In the present work it is demonstrated on the basis of the soft anatomy that the taxa added to *Callistoplepa* since d'Ailly (1896) are not congeneric, but are in subfamily Achatininae.

Bequaert & Clench (1934c:114) were misleading when they reported that *C. barriana* and *C. shuttleworthi* 'are from Upper Guinea'. Columbia Lippincott Gazetteer (1952) defines Guinea as equatorial West Africa from Senegal to Angola, being divided into Upper and Lower Guinea by the Niger Delta. van Bruggen (1989) supports the interpretation that the division is at the Dahomey Gap. In either interpretation, these species are limited to Lower Guinea. d'Ailly (1896:70) states that both species live in small numbers in shady places at the base of tree trunks and under detached pieces of bark.

Key to Species

Second whorl with thin crescentic threads and granules; last whorl evenly convex, expanding greatly, four times the length of the penultimate whorl when viewed dorsally; aperture length > shell width except in smallest specimens; peripheral arrow-shaped pattern usually pale and diffuse, occasionally absent or nearly so; the suture transects a smaller and often darker pattern; white flecks sparse or abundant, irregularly distributed; nepionic whorls 3; larger species (6 whorls = 38–52 mm long). Genital aperture complex, large, superficial; penial retractor inserts on the right columellar retractor posterior to all other branches; penis tubular; vagina longer than wide. Cameroon, Nigeria *barriana*

Second whorl grossly deeply closely and evenly costate; last whorl subcarinate, expanding proportionately, three times the length of the penultimate whorl when viewed dorsally; aperture length < shell width; conspicuous light castaneous arrow-shaped pattern at periphery, with concentrations of white flecks tending to alternate with the pattern; a smaller similar pattern appears subsuturally, but the white flecks there are more scattered; nepionic whorls 2½; smaller species (6 whorls = 26–34 mm long). Genital aperture simple, small, lacunate; penial retractor inserts on the right columellar

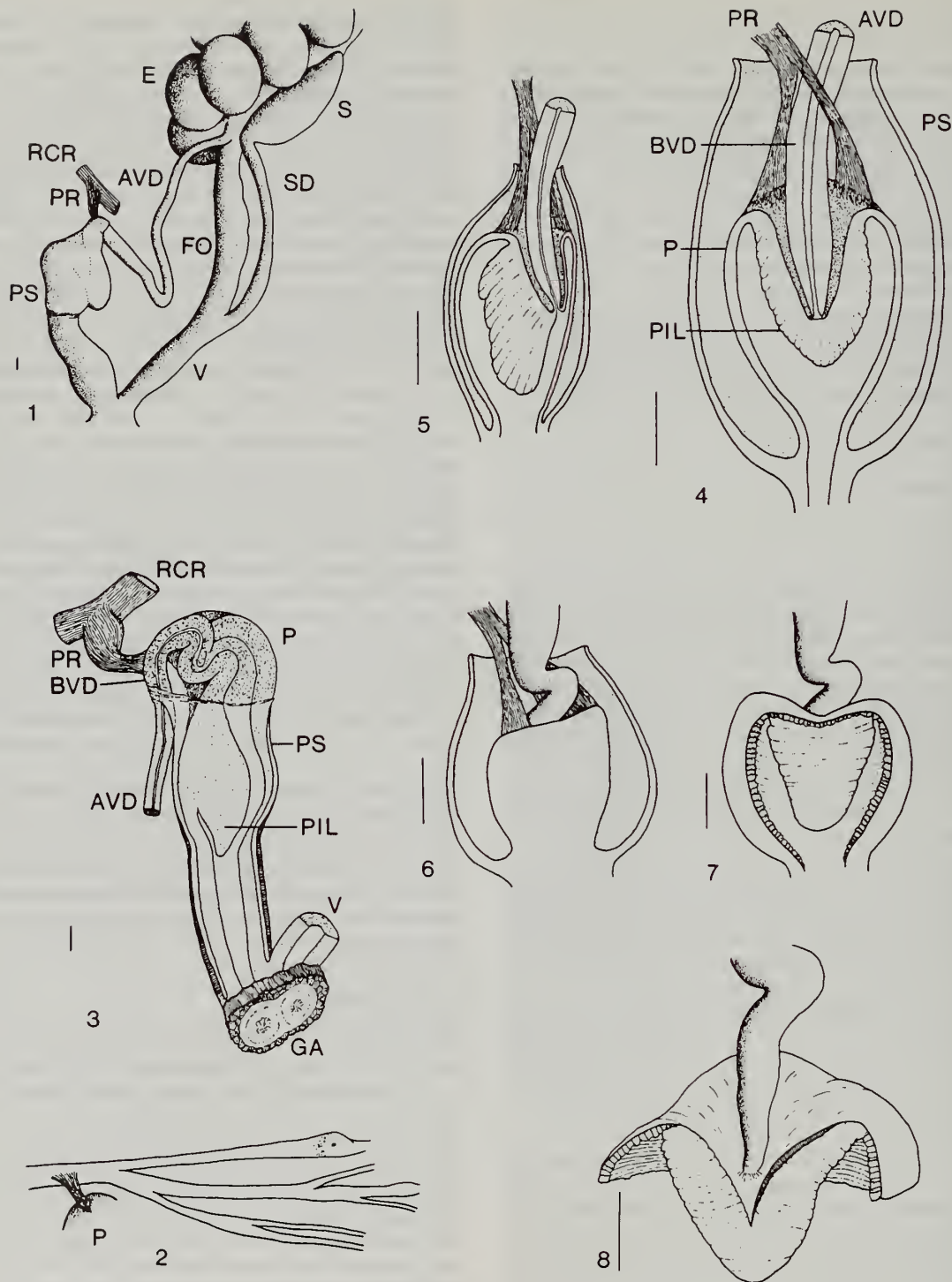


Fig. 1 *Callistoplepa barriana*, basal genital structures (MRAC no. 795.956).

Fig. 2 *C. barriana*, right branch of columellar muscle showing posterior attachment of the penial retractor.

Fig. 3 *C. barriana*, right ventrolateral view of penis to show the pilaster in profile. Contraction during preservation has telescoped the apical penis and forced it and its fibromuscular matrix out of the penis sheath.

Fig. 4 *Callistoplepa shuttleworthi*, penis sheath, permanently partially evaginated penis, and pilaster (containing the basal vas deferens) are shown in frontal plane and in dorsal view (UUZM).

Fig. 5 Same, in a slightly tangential sagittal plane.

Fig. 6 Same, in ventral view with penis sheath cut longitudinally and spread laterally to show the penis within.

Fig. 7 Same, with penis cut longitudinally and spread laterally to expose the pilaster within. Penis sheath not shown.

Fig. 8 Same, with pilaster cut and spread to reveal the basal vas deferens opening dorsally into the lumen of the penis. The dense fibromuscular webbing at the junction of the basal vas deferens and penis has been removed for clarity.

retractor anterior to the retractor of the right optic tentacle; penis permanently partially evaginated; vagina wider than long. Cameroon, Gabon, Equatorial Guinea ('Grand Bas-sam' locality is suspect) *shuttleworthi*

***Callistoplepa barriana* (Sowerby, 1890)**

Figs. 23, 24

Achatina barriana

Sowerby, 1890:579, pl. 56, fig. 2; von Martens, 1891:30.

Ganomidos barrianum

d'Ailly, 1896:70, pl. III, figs. 5–10 (egg), text fig. (radula).

Callistoplepa barriana

Pilsbry, 1904–05:127, pl. 47, figs. 14–17 (egg), pg. ix fig. 2, pg. xv (radula, ex d'Ailly); Germain, 1909:90; Bequaert & Clench, 1934c:114.

Ganomidos barrianum

Boettger, 1905:170.

Callistoplepa barriana

Dautzenberg, 1921:98; Oliver, 1983:9 (syntype).

SHELL. Shell ovate-conic, very thin, fragile, translucent, shiny. Whorls 6–6¼, rarely 6½, moderately convex. The second and third nepionic whorls are nearly straight sided, but they immediately give way to postmergent rapidly expanding whorls, producing a mammillate or submammillate, broadly conic spire and a blunt apex. Shallow sutures form a thin, nearly even line. Last whorl large, convex, 82% of shell length, range for 4–6½ whorls = 78–86% ($n = 115$), swelling faintly outward directly below the suture in some specimens. Aperture broadly ovate, nearly vertical, pale milky within. Columella thin, slender, slightly to broadly arcuate, concolorous, squarely to obliquely truncate, inner rim rolled adaxially. Outer lip thin, nearly evenly arcuate; joining the periphery at only a modestly acute angle; greatest width is characteristically midway. Parietal callus scarcely apparent in unweathered specimens.

From apex to base, the shell ground collar is uniformly pale fulvous. Superimposed on this, beginning imperceptibly in the fourth whorl, are two narrow bands of slender yellow-brown chevrons – one at the periphery, and a less distinct one transected by the suture. The chevrons in close juxtaposition have their apices oriented prosocline and are about as wide as the space between them. Much thinner, more irregular, paler, parallel sinuate stripes may join the two bands. Specimens with the most conspicuous patterns may have a second zone of thin, pale, transverse bands between the periphery and the base of the shell. The peripheral pattern tends to fade with increased growth. Some specimens may have present only the sutural band, or a unicolorous last whorl, or an entirely unicolorous shell except possibly for a slightly darker transverse band laid down between growth periods. Any of the whorls may be flecked with minute circular or elongate white spots (usually ca 0.2–0.8 mm). These are irregularly and sparsely dispersed, but are especially conspicuous within the costae of the last whorl. Upon close examination, they are seen to be a consolidated white powdery substance between the two periostacal layers. Although some are associated with shell injuries, their formation is apparently a natural phenomenon contributing to cryptic coloration.

The most apical portion of each nepionic whorl dips abruptly at near-right angles adaxially to form a narrow platform in which is embedded a strikingly uniform series of minute shallow pits that fringe the suture. This ornamenta-

tion is limited to the nepionic whorls and is the homologue of the diagnostic grossly costate sculpture in the second nepionic whorl of *C. shuttleworthi*. The first whorl is essentially smooth. Short faint slender crescentic threads and granules, oriented transversely but aligned spirally in irregular series, gradually make their appearance in the second whorl. As this sculpture becomes more organized, the spaces between the several spiral series seem to form shallow spiral striae. Near the junction of the third and fourth whorls, a sharp transverse delineation marks the end of the nepionic whorls, at which level the threads become more symmetrical and greatly compressed, but retain their individuality. With continued growth, the threads remain fairly distinct or become transversely variously fused into costellae, which interrupt or obliterate in part the shallow spiral striae. Gradually the threads become more bold and evolve into slender, closely and very evenly placed prosocline corrugations or costae, commonly with splitting and anastomosis. The spiral striae remain superficial, barely transecting the costae. The depressed cancellate sculpture below the periphery of the upper whorls gradually becomes more corrugate until an essentially uniformly costate sculpture is finally formed on the entire forward last whorl of the fullgrown specimen, diminishing slightly toward the columella and obliterating the peripheral line of demarkation. The smallest shells may be vaguely subcarinate.

SOFT ANATOMY. Alcohol preserved specimens available 31/dissected 13. Nigeria: BMNH 1/1; Cameroon: MRAC 2/2, SMNH 10/4, SMF 14/6, UUZM 4/0. d'Ailly (1896) had access to 34 alcohol-preserved specimens collected in Cameroon by P. Dusén, Y. Sjöstedt and J.R. Jungner. With the generous assistance of Dr Åke Franzén, a diligent search was made in the museums of Stockholm and Uppsala in 1987, but only 14 specimens could be found. There was no evidence of Jungner's specimens.

The body of the preserved specimen is uniformly grey fulvous, without any apparent markings. Immediately posterior to the shell, there is a depressed plateau that is fringed by two prominent dorsolateral ridges, each composed of 12 closely aligned, truncate incisor-shaped elevations.

The most unusual feature of the internal anatomy of this species is the penis sheath (PS) (Fig. 1). Thickest at its base (~0.5mm) it diminishes apically to a diaphanous fascia (~0.05 mm) that, in the normal position, enshrouds the apical penis (P), the most basal part of the vas deferens (BVD), and the basal portion of the extraordinarily short penial retractor (PR). As in other achatinids, the origin of the PR marks the division between P and BVD. In contrast to that in *C. shuttleworthi*, the PR inserts on the right columellar retractor (RCR) posterior to all other branches (Fig. 2). In the fully mature specimen (Fig. 1) the tapering attenuated apical P appears to be cramped into a sigmoid fold in this thinnest apical PS. A dense webbing of muscle and connective tissue fibrils, originating from the PR, obscures, entangles and foreshortens the apical folds of the P, even to the point in the oldest specimens where this tight, woolly mass of fibromuscular tissue becomes histologically intimately intermeshed with the substance of the apical penial wall. On its outer surface, this cocoon-like network forms a smooth, dense coating over the P that is completely free from the equally smooth but very shiny inner surface of the PS, thus allowing free movement between P and PS. Basally, where the PS is thickest, this fibrous layer conversely becomes so

thin on the surface of the P and so intricately associated with it, as to be essentially imperceptible. About midway on the P, the PS suddenly goes from thick to thin. This creates a transverse line of thin folds that incorrectly suggests the PS terminates at that level (Mead, 1992, fig. 2). However, when there is extreme contraction during preservation, the apical edge of the PS actually does pass basally far enough to allow the apical structures to elbow out of the PS (Fig. 3). The contraction emphasizes the bipartite nature of the P: an apical convoluted, transparently ensheathed portion and a basal irregularly bulging, opaquely ensheathed portion that contains the pilaster (PIL). Internally, the most basal P is longitudinally plicate; above that, including the PIL, the epithelium is vermiculate-rugate. The PIL is a simple, greatly thickened, longitudinal, roundly elevated ridge of the ventral penial wall that strongly projects dorsally into the lumen of the P. Basally, this ridge terminates into a solid, inverted-conical, pendulous verge-like process. Although its margins are not well defined, axially the PIL has a more gross epithelial texture than the surrounding tissue. The apical vas deferens (AVD) is a conspicuously uniformly slender conduit (~1.0 mm in width). It lacks the heavy muscular basal portion found in *C. shuttleworthi*, thus the physical support for the intromittent organ in *C. barriana* doubtless is provided by the thick, longitudinal P.

The vagina (V) is a short, nearly uniformly wide conduit, about one-third the length of the P. Internally, it is lined with vermiculate-rugate epithelium and is without any apparent modifications at its junction with the spermathecal duct (SD) and free oviduct (FO). The muscular FO is as wide or wider than the V, 2–3 times as wide as the SD, and about as long as the SD. For their full length, both FO and SD are tightly bound to each other by fairly regularly appearing small slips of muscle. The junctions of the AVD/FO and spermatheca (S)/SD are pulled in close juxtaposition by the tissues of the sagittal myoseptum. Just apical to this, the capitate S, about the length of the V, is broadly attached to the basal (uterine) portion of the spermooviduct. The SD is a thin-walled mostly uniformly slender conduit about the caliber of the AVD. Five gravid specimens were examined; three with full data had been collected near the end of the rainy season in October/November. For such a relatively small species, the eggs are quite large (6.8×5.4 – 6.3×5.1 mm). Fully gravid specimens contained 11–15 eggs, all with heavy, calcareous shells and distributed in the full length of the spermooviduct. The ovotestis acini appear in four or five discrete clusters under the columellar surface of the right (apical) lobe of the digestive gland. A talon with a round base and an apical, diverticulate elongation is present.

The genital atrium (GA) in this species is unique among the achatinids so far dissected. It is comparatively large and so shallow that it is essentially a common genital depression, immediately within which appear conspicuously the male and female orifices. These latter, like twin craters, are individually surrounded by low elevated circular walls of smooth tissue, which contiguously fuse at their inner margins (Fig. 3).

TYPE MATERIAL. Sowerby (1890:579) did not designate a holotype. The BMNH specimen '89:11.19.2 purchased of Sowerby' is here designated the lectotype (Figs. 23, 24; Table 1). The slightly damaged and trimmed second syntype, NMW, 1955:158.832 in the Melvill-Tomlin collection is here designated a paralectotype (Oliver, 1983). Remeasurements

of the lectotype confirm Sowerby's figures except for the shell length, which is 41.0 mm rather than '43 mm'. Sowerby's illustration is so poorly rendered that it is not precisely identifiable with either syntype.

TYPE LOCALITY. 'Calabar, Africa?' Nigeria, 4° 57' N, 8° 19' E. J.C. Reid of the University of Calabar recently confirmed this queried locality. Although he has made many excursions into the 'relatively undisturbed Oban Hills Forest which yields a rich fauna', he found only two (live) specimens along a permanent stream at Aking (= Awsawmba) 5° 26' N, 8° 38' E, 78 km northeast of Calabar. One of these specimens (BMNH) was examined anatomically and conchologically in the present study and was found to be typical; the second specimen is reportedly in the Tom Pain collection (NMW).

DISTRIBUTION. This species has been found essentially along the entire expanse of coastal Cameroon from M'Bonge (= Bonge) 4° 33' N, 9° 05' E in the north to Itoki 2° 24' N, 9° 50' E in the south. Most of the known twenty localities are clustered in northwestern Cameroon, spilling over into southeastern Nigeria and extending inland as far as Yaoundé 3° 52' N, 11° 31' E; Métet 3° 05' N, 11° 00' E; Ebolowa 2° 54' N, 11° 09' E and Sangmélima 2° 56' N, 11° 59' E. The nine other localities are in the environs of Victoria 4° N, 9° E. In all localities, seven were shared with *C. shuttleworthi* and five were shared with *Leptocala mollicella*. Only a single general locality record was found for Gabon (Verreaux, 1855 NHMB) and no record for Equatorial Guinea; but this species eventually probably will be found to be limited to the northern regions of these two countries. Data labels indicate that specimens were collected in plantations in Kumba 4° 38' N, 9° 25' E (bananas), Missellele 4° 07' N, 9° 25' E (coca), 'Buenga' (oil palm), and in primary forests.

Table 1 *C. barriana* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Width	% whorl	% LW/L	% W/L	
6¼	59.0	32.4	36.1	19.5	49.0	82	55	Bonge (UZZM)
6¼	57.5	30.0	32.8	16.9	46.0	80	52	Victoria (ZMB)
6	50.7	27.8	30.9	16.8	41.9	83	55	Idenau (SMF)*
6	49.0	29.9	30.6	17.5	40.8	83	61	Bonge (SMNH)
5¾	44.0	27.4	29.6	16.3	37.8	86	62	Bonge (SMNH)
6	41.0	23.3	24.9	14.5	32.3	79	57	Calabar (BMNH) Lect <i>A. barriana</i> *
6	41.0	22.8	26.6	13.4	34.0	83	56	Kumba (MRAC) 795.173
5½	36.8	23.0	23.6	13.4	29.8	81	62	Idenau (SMF)
5	25.2	15.3	16.4	8.8	20.6	82	61	Bibundi (SMF)
4¾	20.5	13.8	13.2	7.6	16.8	82	67	Bibundi (SMF)

Total specimens examined: 125. Sources: BMNH, CMNH, IRSN, MCZ, MNHN, MRAC, NHMB, NHMW, NMW, SMF, SMNH, UHZI, UZZN, ZMB, ZSM.

REMARKS. This species is commonly encountered in collections and often confused with immature *Achatina bandeirana* Morelet, 1866 and *A. craveni* E.A. Smith, 1881, both of which have a proportionately much smaller last whorl.

***Callistoplepa shuttleworthi* (Pfeiffer, 1856)**

Figs. 25, 26

Achatina shuttleworthi

Pfeiffer, 1856:34, 1859:603, 1868:216, 1877:275.

Callistoplepa shuttleworthiana

Ancey, 1888:69.

Ganomidus shuttleworthi

d'Ailly, 1896:69, pl. 3, figs. 11–14, text fig. (radula).

Callistoplepa shuttleworthi

Ancey, 1898:92; Thiele, 1929:560, fig. 644 (radula).

Callistoplepa shuttleworthi

Pilsbry, 1904–05:127, pl. 47, figs. 18–20, pg. xv (radula, ex d'Ailly); Germain, 1909:90, 1916:248, pl. 10, fig. 4; Bequaert & Clench, 1934b:114; Ortiz & Ortiz, 1959:45, pl. 5, figs. 97, 98, text figs. 28–31 (genit. syst., pallial complex, jaw, radula); Zilch, 1959:373, fig. 1352.

Ganomidus shuttleworthi

Boettger, 1905:170.

SHELL. Shell elongate-ovate, extremely thin, very fragile, translucent with a subdued gloss. Whorls $5\frac{1}{2}$ – $5\frac{3}{4}$, rarely 6, noticeably flattened in profile. A somewhat restricting, deeply cut second nepionic whorl produces a mammillate obtuse apex. The following whorls form a slender conic spire as they descend more rapidly than they expand. Sutures between nepionic whorls are deep and regular; those between postemergent whorls are more shallow and only slightly irregular. Last whorl subcarinate, noticeably so in juvenile specimens, expanding proportionately, 77% of shell length, range for $4\frac{1}{2}$ –6 whorls = 73–83% ($n = 60$). Aperture oblique-ovate, external colour pattern sharp and distinct from within. Columella usually straight, axial, rarely slightly arcuate, inner rim erect with a cord-like thickened crest; truncation oblique to very oblique, rarely at right angles. Between the third and fourth whorls, the crest of the columella rolls abaxially on itself to form a hollow tube, therefore an open umbilicus. Between the fourth and fifth whorls, this tube narrows and solidifies to form a slender axial cord, which is seen in the full grown shell. This series of changes, from open to closed, enigmatically has been observed in several disparate achatinid species, e.g. *A. achatina* (Linné, 1758) and *Archachatina* spp. Outer lip of shell thin, skewed basally, joining the periphery at an acute angle; greatest width below midway; this is emphasized by the subcarinate nature of the shell. Parietal callus thin, vague.

Shell ground colour is pale corneous. The first $2\frac{1}{2}$ whorls are unicolorous. Starting near the third whorl, vague roundish, very pale castaneous spots appear both at the suture and periphery. At these two levels, the spots quickly assume sharply angulate prosocline arrow-shaped patterns, highlighted with a series of parallel transverse elongate white flecks. Similar flecks, reminiscent of those in *C. barriana*, are scattered irregularly over the shell above the periphery, rarely below. Soon the sutural band fractionates and moves increasingly into a subsutural zone. The large arrows at the periphery become spirally closely juxtaposed to form an essentially continuous dominating colour band. From it, slender, nearly parallel light castaneous stripes pass sinuously

to the subsutural band and transversely to the columella.

Only rudimentary costae appear in the last part of the otherwise smooth first whorl. The entire second whorl is conspicuously and uniformly ribbed from suture to suture with elevated, deeply cut, nearly orthocline, gross costae, ca 0.2 mm wide (cf Germain, 1916 pl. 10, fig. 4). In the third whorl the now more prosocline costae are soon reduced to half their width. At midway in this whorl, an interruption in the alignment of the costae marks the end of the nepionic whorls. Gradually the costae become wider and finally regain their original width in the fifth whorl, only to become narrower and somewhat irregular in the last part of the sixth whorl. Faint shallow closely spaced spiral lines, starting in the second whorl, almost imperceptibly transect the prominent costae. There is a delicate, greatly suppressed cancellate-granulate sculpture on a vitreous surface below the periphery in the upper whorls. This is invaded by the costae in the sixth whorl until the entire whorl from suture to columella is nearly uniformly costate. No splitting or anastomosis of the costate has been observed.

SOFT ANATOMY. Alcohol preserved specimens available 12/dissected 5. Cameroon: SMNH 5/2, UUZM 7/3. All specimens were collected by Y. Sjöstedt. The only two extant mature specimens were found by Å. Franzén in a medical laboratory at UUZM. d'Ailly (1896) reported having access to 11 alcohol preserved specimens, which apparently did not include Sjöstedt's Itoki specimens that were available in the present study.

Body colour as in *C. barriana*; spade-shaped elevations on the posterior foot only slightly less prominent.

Without having dissected and deciphered first the relatively more simple reproductive tract of *C. barriana*, it would have been very difficult to interpret the relationships of the genital structure in this species. In essence, the axis of the basal male conduit has been greatly foreshortened telescoping the homologous structures to such an extent that the pilaster (PIL) on the ventral wall of the penis (P) is pivoted 180° , forcing the junction of the P and basal vas deferens (BVD) deeply into the dorsal aspect of the infolded P, i.e., the upper ventral wall of the P and the most basal part of the BVD are therefore seen only in the dorsal or lateral views (Figs. 4, 5). A dense network of muscle and connective tissue fibrils firmly fixes the structures in this permanently partially evaginated position. This places the aperture of the BVD and the contiguous subapical part of the PIL into a basal position within the folded penial wall to take the lead in forming the intromittent organ at extroversion. The inner smooth shiny surface of the extremely thin-walled penis sheath (PS) facilitates seriatim extroversion: PIL-P-PS and finally genital atrium, with the BVD and the attenuated penial retractor (PR) contained axially within the intromittent organ. Figures 6, 7, 8 show at progressively deeper levels of dissection these relationships from the ventral view. Both PIL and the inner penial wall are confluent with a deeply rugate epithelium. It should be noted that since the BVD opens directly into the lumen of the penial chamber rather than passing through the accessory organ to open at its apex, a pilaster rather than a verge (penis papilla) is formed.

The PR is extremely short and, as in the other species of Callistoplepinae, it and the BVD are held tightly together by the PS apical to the completely enclosed P (Fig. 9). In contrast to that in *C. barriana*, the PR inserts on the right columellar retractor (RCR) anterior and strongly ventral to

the retractor of the right ommatophore (RRO) (Figs. 10, 2). Ortiz & Ortiz (1959) missed the diminutive PR in their dissections and do not show it in their illustrations. Emerging above the PS, the apical vas deferens (AVD) is a large muscular thick-walled conduit that in its normal position reaches to the penio vaginal angle and doubtless serves both as an ejaculatory duct and a physical support for the intromittent organ. Apical to this, the conduit narrows to half the calibre and is thinner walled.

The vagina (V) is very short, but two to four times wider than its length. Near its base, sparse, thin muscle strands suggest a primordial vaginal retentor. Internally, the V is muscular, thick-walled and longitudinally deeply plicate. There is no sharp delineation between it and the broad, somewhat thinner walled basal spermathecal duct (SD). This latter is so large that it tends to be positioned partly between P and V. Both upper SD and free oviduct (FO) are thin-walled and of about the same calibre. The clavate spermatheca (S) is broadly attached to the spermoviduct apical to the AVD/FO junction. The ovotestis acini are as in *C. barriana*. No specimen was found to be gravid, but a single specimen collected in October in Bonge seemed to be near it with a very large albumen gland and an inflated spermoviduct. Ortiz & Ortiz (1959) examined a single specimen from Fernando Póo Island (Macías Nguema Biyogo) and found the spermoviduct completely crowded with four comparatively large white eggs. Seven dried eggs (MCZ no. 219224) measured in the present study average 4.7×3.7 mm. A diminutive talon is present. In contrast to *C. barriana*, the genital atrium is an inconspicuous dimple without superficial embellishments.

TYPE MATERIAL. Pfeiffer (1856) described this species from Cuming collection specimens, giving the shell size as $5\frac{1}{2}$ whorls and the length-width measurements as 34×17 mm; later (1859) he gave aperture measurements as 19×11.5 mm. The measurements of the three syntypes in BMNH do not match those of Pfeiffer, but are reasonably close. The largest syntype has a damaged and repaired last whorl and the next largest is atypically slender; therefore the smallest specimen (Figs. 25, 26; Table 2) is here selected as the lectotype, the other two becoming paralectotypes. No convincing evidence was found that other syntypes are extant. Only four other specimens of the 60 examined in the present study exceeded 30 mm in shell length.

TYPE LOCALITY. The syntypes in the Cuming collection were reported to be from "Grand Bassam" *Africae occidentalis* (Verreaux). All other specimens examined bearing this locality were sold by shell dealers, viz. Da Costa, Fulton, Geret, Paetel and Preston, who may have taken their cue for a locality from the original description. No museum specimen has been found with a locality record from the 1400 km stretch of continental Africa between Grand Bassam, Ivory Coast and the cluster of reliable locality records in northwest Cameroon. It is suspected that this is a case of still another erroneous Cuming record. Although under the circumstances, we must accept the type locality as 'Grand Bassam', it is probable that Cuming's specimens came from Cameroon, or perhaps Gabon. The likelihood of an early secondarily established population in Grand Bassam prior to 1856 is extremely remote, for surely authentic collecting records would have appeared in the meantime. Edouard Verreaux (cf Crosse & Fischer, 1869) not only collected the syntypes of this species, but he also collected the single known specimen

Table 2 *C. shuttleworthi* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl	% LW/L	% W/L	
6	34.0	18.7	18.4	10.3	26.4	78	55	'G. Bassam' (MCZ) 83441
6	32.3	18.4	18.4	10.0	24.5	76	57	'G. Bassam' (BMNH) PLec
6	31.0	16.7	16.4	9.0	22.8	73	54	'G. Bassam' (BMNH) PLec
5 $\frac{3}{4}$	30.9	18.3	17.0	10.7	24.0	78	59	'G. Bassam' (BMNH) Lect A. <i>shuttleworthi</i> *
5 $\frac{3}{4}$	26.9	15.8	14.8	8.0	20.7	77	59	Edea (MCZ)
5 $\frac{1}{2}$	24.1	14.8	14.4	8.0	19.0	79	61	Gabon (MRAC) 5314 (Preston)
5 $\frac{1}{2}$	22.9	13.0	12.1	6.8	17.3	75	57	Bibundi (SMNH)
5 $\frac{1}{4}$	20.2	11.5	11.8	6.8	16.1	80	57	Itoki (UUZM)*
5	19.4	11.4	11.2	5.9	15.4	79	59	Bibundi (SMF)
4 $\frac{1}{2}$	16.0	10.5	8.9	5.3	12.5	78	66	Gabon (IRSNI) (Vignon)

Total specimens examined: 60. Sources: BMNH, GNM, IRSN, MCZ, MNHN, MRAC, NHMW, SMF, SMNH, UMMZ, USNM, UUZM, ZMB.

of *C. barriana* from Gabon, now in Bern (NHMB). This raises the suggestion that Verreaux, after collecting in Gabon and Cameroon, shipped his specimens from Grand Bassam, which Cuming assumed was the collecting site.

DISTRIBUTION. Leonardo Fea was the first to discover this species on Fernando Póo Island (= Macías Nguema Biyogo) of Equatorial Guinea $3^{\circ} 30' N$, $8^{\circ} 40' E$ (Germain, 1916:249). Subsequently, Ortiz & Ortiz (1959:45) reported it from Basilé and Mongola on that island. Nine reliable localities on the mainland in Cameroon define a limited coastal belt, ca 280×120 km with N'dian $4^{\circ} 55' N$, $8^{\circ} 53' E$ in the north; Métet $3^{\circ} 05' N$, $11^{\circ} 00' E$ in the east; and Itoki $2^{\circ} 24' N$, $9^{\circ} 50' E$ in the south. Other Cameroon localities: Albrechts Höhe $4^{\circ} 38' N$, $9^{\circ} 25' E$; Mukonje (= Mukonye) $4^{\circ} 37' N$ $9^{\circ} 30' E$; Bibundi $4^{\circ} 13' N$, $8^{\circ} 59' E$; Edéa $3^{\circ} 48' N$, $10^{\circ} 08' E$; Lokoundje $3^{\circ} 13' N$, $9^{\circ} 55' E$. A specific locality record for Gabon was not found, but Vignon, through Ancey (1888:69), reports them as rare in Gabon at the edge of forest streams. They probably do not extend south of the Ogooué River.

Callistoplepa tiara Preston, 1909 – A Misidentification

Preston (1909:183, pl. vii, fig. 9) described *Callistoplepa tiara* from 'Bitze [= Bitye], near the River Ja [Dja], Cameroons' ($3^{\circ} 01' S$, $12^{\circ} 22' E$). He indicated neither the collector nor the number of specimens he had; however, some specimen labels (BMNH, MRAC) specify that G.L. Bates was the collector. Between 1908 and 1912, Preston distributed ten known syntypes, each bearing the full locality information

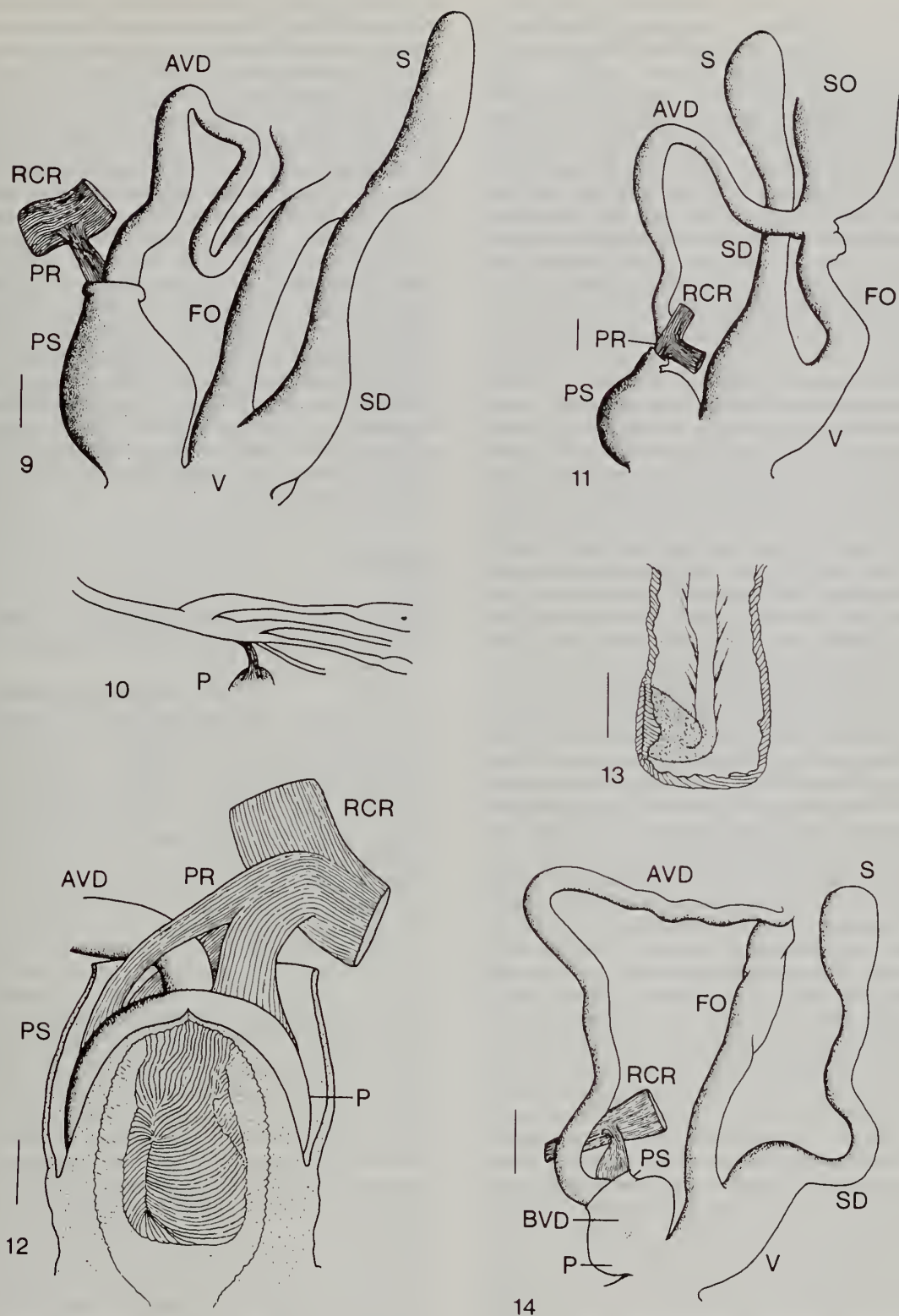


Fig. 9 *C. shuttleworthi*, basal genital structures (UUZM).

Fig. 10 *C. shuttleworthi*, right branch of columellar muscle showing anteroventral attachment of the penial retractor.

Fig. 11 *Leptocala mollicella*, basal genital structures (MRAC no. 796.850).

Fig. 12 *L. mollicella*, penis sheath, penial retractor and penial wall cut longitudinally and spread to reveal the pendulous pilaster within (MRAC no. 795.638).

Fig. 13 Same, cutaway of pilaster to show basal vas deferens joining the penial sacculus, which leads to the aperture of the pilaster.

Fig. 14 *L. petita*, basal genital structures (MRAC no. 214.044).

and Preston as the source. These syntypes are currently to be found in the following museums: BMNH (3: no.1908.7.1.13-14, and MacAndrew Coll.), NMW (Melville-Tomlin Coll. no.1955.158.826; Oliver, 1983:1), IRSN (Dautzenberg Coll. no.169), ZMB (no.62345), MNHN, MRAC (no.5760), RMNH, UMMZ (Bryant Walker Coll. no.142031). These vary in size from $6\frac{1}{2}$, 63.0×31.3 to $5\frac{1}{2}$, 44.2×25.7 . Preston probably placed his presumed new species in *Callistoplepa* because of the very thin shell, the Cameroon type locality, and the fact that the size, general shape and peripheral colour pattern of his specimens were reminiscent of *C. barriana*. However, upon examination of the shell sculpture in the present study, all syntypes were found to be juvenile *Achatina bandeirana* Morelet, 1860.

In Cameroon, *A. bandeirana* and the closely related *A. iostoma* Pfeiffer, 1854 and *A. balteata* Reeve, 1849 are sympatric and it is not uncommon to find mixed lots of these three species in museum collections. Preston, himself, apparently had a mixed lot from which his syntypes were selected. He sent a 'cotype' of *Callistoplepa tiara* to Dupuis (IRSN, General Coll.); however, its locality record was simply 'Cameroon'. After Dupuis (1923) examined this specimen, he concluded that it probably was a juvenile *A. iostoma*. In 1934, Bequaert also saw this specimen and confirmed Dupuis' conclusion. Their identifications were corroborated in the present study because this 'cotype' specimen revealed the following characters in contrast to those of the syntypes identified as *A. bandeirana*: 1) upper whorls not convex, but form a nearly straight-sided pyramid; 2) apex more acute rather than blunt; 3) a slight but apparent peripheral carina is present in the early whorls; and 4) sculpture is formed by finer, more uniform, elevated beads that do not evolve into minute prosocline arcuate welts in the sixth to seventh whorls (cf Bequaert & Clench 1934a fig. 3). This last character is diagnostic for *A. bandeirana*; but it is inadequately developed in the very immature specimen of five to six whorls, thus such individuals of the three species may appear to be alike.

Dupuis' unique 'cotype' persuaded Bequaert to assume that all syntypes of *C. tiara* were juvenile *A. iostoma* and he so identified them in collections (BMNH, IRSN, ZMB, RMNH) and in his publications (Bequaert, 1950:39; B. & Clench 1934a:13; 1934c:114). Dautzenberg was similarly impressed and was moved to place with his 'cotype no.169' an added notation, 'Erreur de Preston, C'est un jeune *Achatina iostoma* Pfeiffer'. This was unfortunate because Dautzenberg's specimen, with full *C. tiara* field data, is shown now to be an immature *A. bandeirana*. IRSN thus has a true syntype in the Dautzenberg Collection and questionable 'cotype' in the General Collection, which latter is here confirmed to be *A. iostoma* and not a bona fide syntype. A somewhat similar situation exists at BMNH, which has three valid syntypes. A fourth specimen in the Connolly Collection (BMNH no.1937.12.30.3684) was sent by Preston and labelled '*Callistoplepa tiara* Pr.' (apparently in his writing) but without any locality data, except 'Bitz' in the accession book. Connolly had his doubts about the identification and relabelled it '*Achatina ? balteata* Rve juv.' Bequaert also saw it in 1933 and referred to it as *A. iostoma*. This now proves to be still another juvenile *A. bandeirana* and is here considered a doubtful eleventh syntype of *C. tiara*.

It should be noted that *A. bandeirana* is a wide spread, highly variable Lower Guinea species complex involving *A. b. arenaria* Crowley & Pain, 1961; *A. b. mayumbensis* C. & P., 1961; *A. paivaana* Morelet, 1866, (1868); and *A. dohrni-*

ana Pfeiffer, 1870. It is found from Cameroon to northern Angola (7° N- 10° S) and fans north and east into Gabon, Central African Republic, Congo Republic and Zaire. A study of this complex is in progress.

Preston did not designate a type, but he retained in his own collection the specimen that was illustrated in his description of this species. This syntype is here selected as the lectotype (measurements: 6; 49.4×26.7 ; aperture 30.9×13.8 ; last whorl 40.0 mm). It is now in Tervuren (MRAC no.5760) and can be precisely identified by the unique configuration of the map-like pattern on the last whorl. This pattern is caused by the irregular lifting up of the thin outer periostracal layer from the durable inner periostracal layer, allowing an air space between. This produces blotchy grey-white patches, which probably provide cryptic coloration. The juvenile and mature specimens of both *A. bandeirana* and *A. iostoma* commonly have these patches, which have been referred to as 'hydrophanous streaks' (Bequaert & Clench, 1934a:15). They apparently are homologous to the conspicuous white flecks on the shells of *Callistoplepa barriana* and *C. shuttleworthi* and may have contributed to Preston's decision to put his species in this genus.

Leptocala

Petitia

Joussemae, 1884:171 (non Chitty, 1857); d'Ailly, 1896:71; Bequaert, 1950:138 (type species: *Petitia petitia* Joussemae, 1884).

Leptocala

Ancey, 1888:70, 1898:92 (type species: *Achatina mollicella* Morelet, 1860); Thiele, 1929:560; Bequaert & Clench, 1934c:116; Ortiz & Ortiz, 1959:24.

Achatina (Leptocala)

Pilsbry, 1904:72; Spence, 1928:213; Bequaert, 1950:138; Zilch, 1959:366; Vaught, 1988:89.

Achatina (Leptocola)

Kobelt, 1910:66 (non Gerstaecker, 1883).

Leptocala (Leptocala)

Bequaert & Clench 1934b:272.

Pilsbry (1904:73, 75) reduced genus *Leptocala* to subgeneric rank in *Achatina* and placed within it his new Section *Leptocallista*. Thiele (1929:560) returned Ancey's *Leptocala* to generic rank and retained within it Sections *Leptocala* and *Leptocallista*. Bequaert & Clench (1934b:274) elevated these sections to genus and subgenus, respectively. In 1950, Bequaert placed both names as subgenera of *Achatina*. Zilch (1959:366) followed suite. The present studies of the soft anatomies demonstrate that these two genus-group taxa are in separate subfamilies because the East African *Leptocallista* is anatomically allied to *Lissachatina* and therefore is an achatinine.

Bequaert & Clench (1934b,c) announced that the Cameroonian *Pseudoglessula efulensis* Preston, 1908 might belong to *Leptocala* and stated that the type could not be located in the British Museum. The holotype (no.5309) and the paratype (no.97435) of this species were found during the present study in Tervuren (MRAC) and clearly proved to belong to the Subulinidae. Ancey (1888:71) incorrectly placed *Achatina polychroa* Morelet, 1866 in *Leptocala*; Bequaert (1950:48) believed it belongs in subgenus *Pintoa* of *Achatina*. A final decision depends upon a study of its soft anatomy.

The ancestral stock of the two closely related, remaining species in this genus, *L. mollicella* and *L. petitia*, probably became separated in fairly recent times by a vicariance event – possibly the development of the Ogooué River.

Because of the unique microsculpture and the somewhat smaller shell aperture, *Leptocala* up until now has escaped suspicion of being closely related to *Callistoplepa*. The genus is limited to the southwestern portion of Lower Guinea from northwestern Cameroon to far western Zaire.

Key to Species

Shell 6–6½ whorls; spire conic; exceedingly fine distinct vertical and spiral lines form shallow minute engraved rhomboids. Pilaster verge-like, cylindrical, vertically suspended from the apex of a dome-shaped penis; basal vas deferens obscured by penial retractor. North of Ogooué River in Gabon, Equatorial Guinea, Cameroon and probably south-eastern Nigeria *mollicella*
 Shell 6½–7 whorls; spire slender conic; exceedingly fine closely appressed vertical vermiculate-granulate sculpture obliterates the spiral lines, especially on the upper whorls. Pilaster potato shaped, somewhat compressed, attached for nearly its full length along a diagonal right ventrolateral axis of a hull shaped penis; basal vas deferens conspicuous in ventral view. South of Ogooué River in Gabon, Congo Republic, western Zaire and probably Cabinda, Angola- *petitia*

Leptocala mollicella (Morelet, 1860)

Figs. 27, 28

Achatina mollicella

Morelet, 1860:189; Pfeiffer, 1868:216; 1877:275; Vignon (in Ancy, 1888:70); Pilsbry, 1904:29.

Achatina pulchella

von Martens, 1876:258, pl. 3, figs. 1, 2 (syntype) (*non* Spix & Wegner, 1827; *non* Pfeiffer, 1857); Ancy, 1888:70; Pilsbry, 1904:73, pl. 34, fig. 14 (ex von Martens).

Leptocala mollicella

Ancy, 1888:70, 1898:92; Thiele, 1929:560; Bequaert & Clench, 1934b:273.

Achatina smithi

Sowerby, 1890:579, pl. 56, fig. 3 (holotype, monotypy; *non* Craven, 1880).

Achatina sowerbyi

E.A. Smith, 1890:392 (new name for *A. smithi*).

Petitia pulchella

d'Ailly, 1896:71; Boettger, 1905:170.

Achatina (Leptocala) mollicella

Pilsbry, 1904:73; Spence, 1928:213, pl. 2, fig. 5; Bequaert, 1950:138; Zilch, 1959:366, fig. 1342.

Achatina (Leptocala) pulchella

Germain, 1916:154, 241, pl. 6, figs. 11, 12.

Leptocala (Leptocala) mollicella

Bequaert & Clench, 1934b:273.

Leptocala mollicella zenkeri

Bequaert & Clench, 1934c:118, pl. 1, figs. 5–7, pl. 2, fig. 13 (holotype, 3 paratypes).

Leptocala mollicello zenkeri

Bequaert & Clench, 1934c:119 (*lapsus calami*).

Achatina (Leptocala) mollicella petitia

Bequaert, 1950, pl. 58, fig. 4.

Achatina (Leptocala) mollicella zenkeri

Bequaert, 1950:138.

Leptocala pulchella

Ortiz & Ortiz, 1959:25, pl. 5, fig. 99.

SHELL. Shell obovate, glossy, translucent, thin but sturdy; periostracum tenaceous. Whorls 6–6½, moderately convex. Spire conic; apex broadly obtuse; sutures moderately deep, fine, straight or slightly irregular. Last whorl expanding at a somewhat greater rate than the upper whorls, 72% of shell length, range for 4¾–6½ whorls = 69–75% (n=34). Aperture elongate inverted ear-shape, pale milky within. Columella short, variably straight to slightly arcuate and twisted, transversely to obliquely truncate, basal crest slightly elevated in juvenile specimens. Outer lip thin, joining the periphery at a broadly acute angle. Parietal callus minutely granular, shiny, concolorous.

Shell ground colour is pale fulvous, rarely somewhat darker. Most specimens have a distinct but subdued pattern of pale yellow-brown, slender, strongly parallel, nearly straight or somewhat sinuous stripes, usually 0.2–0.3 mm wide, alternating with ground colour bands of about the same width. The banding may be slightly coarser and more conspicuous in the fifth whorl and above. Often apparently unicolorous or weathered specimens under proper lighting and magnification will be seen to have this characteristic pattern at least in limited areas. This is witnessed in Bequaert & Clench's (1934c) figure 7 of their *Leptocala mollicella zenkeri*, which they report is 'without any darker markings'.

The first 1–1½ whorls are smooth and very shiny. Short vertical or arcuate lines begin to appear in the second whorl, often concentrated at the suture below. These soon elongate into delicate, narrow, closely packed vertical lines that span the full width of the whorl. At 2½ whorls, there is a conspicuous diagonal demarkation between the nepionic and the postemergent whorls. At this demarkation, spiral lines that immediately previous to this were sparse, short and ghost-like, quickly form 35–40 nearly evenly spaced exceedingly shallow, but sharply engraved lines. These lines cross the vertical lines and cut the surface into minute engraved rhomboids (see Bequaert & Clench, 1934c fig. 13). In the following whorls, these spiral lines become more numerous and somewhat wavy, suggesting the surface had been evenly and shallowly combed. Beginning at 2½ whorls, subtle prosocline, more sparse growth wrinkles compete with the vertical lines; these may impact the suture directly or arcuately. There is little reduction in the intensity of this engraved pattern below the periphery, although there is a slight reduction in caliber. In the last half of the last whorl, the rhomboid pattern may essentially disappear, leaving the growth wrinkles to dominate. Throughout, the shell characteristically remains remarkably smooth and shiny. A subcarina is present in the early whorls, but this disappears in the fifth whorl.

SOFT ANATOMY. Alcohol-preserved specimens available 12/dissected 4. Cameroon: MRAC 3/3, UHZI 1/0; ZMB 7/0; ZMUC 1/1.

Body colour of preserved specimens, including the head and anterior edge of the mantle, is pale-cream fuscous. Dorsally, there is a diffuse grey wash that shades darker anteriorly. A 1–2 mm wide dark gray band with diffuse borders, appears immediately behind the ommatophores and extends posteriorly along the middorsal neck to the edge of the mantle. Surface of body reticulate-microtuberculate. Foot without structural elaborations.

The most prominent feature of the genital system (Fig. 11) is the massive, muscular basal female conduit that seems to be an ill defined fusion of vagina (V), spermathecal duct (SD) and free oviduct (FO). Sessile to this, obliterating the penio-vaginal angle, is the contrastingly short, broad penis sheath (PS). Crowded together and projecting from the apical collar of the PS are the long apical vas deferens (AVD) and the very short penial retractor (PR). In fact, this latter is so short that only its insertion on the broad right columellar retractor (RCR) may be seen. Like that of *L. petitia* and *Callistoplepa barriana*, it inserts far posterior on the RCR (Fig. 2). The tripartite AVD starts as a slender tube, but soon enlarges to form the thick-walled ejaculatory duct. This in turn narrows and then once again enlarges into a thin-walled conduit (possibly a secondary seminal vesicle) before fusing with the FO to form the spermoviduct. When the PS is cut longitudinally, it is found to be extremely thin and attached basally only about half way down on the stubby, dome-shaped penis (P). Both the inner surface of the PS and the outer surface of the P are smooth and shiny, facilitating extroversion. In this aspect, the PR is seen to hood over the apical P and, about one-quarter the way down, blend with the substance of the thick-walled P. When the PR is split longitudinally and its muscle bands spread apart (Fig. 12), the basal vas deferens (BVD) is seen within, discreet and without muscle or connective tissue attachment. Vertically cutting the penial wall reveals a conspicuous, pendulous, vertically oriented pilaster (PIL) whose thick transverse-diagonally textured brownish, glandular epithelium is continuous with the inner wall of the penis. Ventrolaterally on the PIL is a 1 mm vertical eccentric apertural slit. This leads internally to a funnel shaped penial sacculus, which joins the extension of the BVD in a dense mass of connective tissue. It is clear at this point that the PIL has been formed by a permanent partial eversion of the P. In the process, the basal-most BVD, with its diagonal anchoring muscle strands, forms the axial conduit of the PIL (Fig. 13). During extroversion, to form the intromittent organ, the PIL would take the lead, followed by the basal P, and finally the PS, which would contain the BVD, PR, and a portion of the RCR. Both PR and RCR would be involved in the introversion process.

The alignment of the V, SD and FO insures that the intromittent organ will be channeled directly to the SD. This has been accomplished not only by a large knob of tissue eccentrically blocking the narrow lumen of the FO, but also by a massive buildup of muscular tissue surrounding the large lumen of the basal SD. These modifications, in turn, tend to wedge the SD between P and FO (Fig. 11). Internally, there is a sharp division between the thick-walled, heavily muscular V, with its many narrow, tightly compressed, vertical plicae, and the thick-walled basal half of the SD (functionally an extension of the V), with its several bold, deep, coarse vertical plicae. Cutting across these latter plicae are transverse vermiculate rugae that produce a grossly serrate texture on the crests of the plicae. This rough texture seems to complement that of the P and PIL. All these structures obviate the necessity of a distinct muscular vaginal retentor found in many species of Achatininae. The apical SD is thin-walled, as is the clavate spermatheca (S). The apical saccular FO probably serves to hold the large egg immediately before expulsion; basally, however, it is thick-walled, with a narrow lumen. An 'elbow' tends to form at the junction of the two parts. The lower portion and the collar-like thick-walled V doubtless serve as an ovijector.

Three of the four dissected specimens had the uterus and oviduct crowded with 4, 6 or 8 relatively large, off-white hard-shelled eggs, measuring 4.3×3.7 – 5.1×4.4 mm. Their long dimension is ca. 15% of the adult shell length, which is in strong contrast, for example, to that relationship in *Achatina achatina* at ca. 5%. All gravid specimens were collected September–November, just before the long dry season, and because of the demands of producing eggs, they manifested considerable emaciation, especially in the digestive system. Such observations raise the unanswered question of longevity in this small species. In a single specimen, six ovotestis acini were found under the columellar surface of the apical lobe of the digestive gland. The talon is extraordinarily long and slender and without a basal enlargement.

TYPE MATERIAL. The type of Morelet's *Achatina mollicella*, collected by Vignon, has never been illustrated and its very existence has been uncertain. It is not in the Morelet material in the Paris, Geneva or Tervuren collections. Fulton (1920) reported that he had purchased the Morelet land and freshwater shells in 1892, including 'all the types', but that in transit between Dijon and London many of the fragile specimens, including some types, were broken. The BMNH accession book under date 2 April 1893 confirms this information. It lists the accessioned types (pp. 230–254, 2049 entries) including a single entry indicating that there were only two specimens: '93.2.4.119–120 *Achatina mollicella*, Gabon'. However, neither of these two syntypes have the length-width measurements of '18 × 12 mm' given by Morelet (1860) for an individual 6 whorl specimen. Under the circumstances, it is most likely that the 6 whorl syntype is the one Morelet had in hand. Further, there clearly is an error in his reported measurements because in the 35 specimens examined in the present study, the shell width averages 52% of shell length, not 67% as would be the case if Morelet's measurements were correct. For these reasons, the larger syntype BMNH no.93.2.4.119 is here selected as the lectotype (Figs. 27, 28; Table 3) and BMNH no.93.2.4.120 selected as paralectotype. Morelet's incorrect measurements have contributed greatly to the confused synonymies of his valid species and Jousseaume's valid species *Petititia petitia*.

The lectotype and 10 paralectotypes of von Martens' junior subjective synonym *Achatina pulchella* are in Berlin (ZMB; Kilius, 1992), type locality Bonjongo, Cameroon. Additional single specimens here designated as paralectotypes have been found and labeled in Stockholm (SMNH no.4282) and Tervuren (MRAC no.5315). The holotype (monotypy) of Sowerby's junior subjective synonym and junior primary homonym *Achatina smithi* no.89.11.18.1 is in London (BMNH), type locality 'Calabar, Africa?' The holotype of Bequaert & Clench's *Leptocala mollicella zenkeri* (1934c fig. 6) plus two paratypes (their fig. 7 and one unfigured) are in Berlin (ZMB; Kilius, 1992). A third paratype is at Harvard (MCZ) under No. 98687, which was identified by the distinctive mark at the junction of the ultimate and penultimate whorls (cf. their fig. 5). All these were from Yaoundé. A fourth paratype, unfigured but listed on their page 119 is from Bitye (BMNH, no.1908.6.3.2; Table 3).

TYPE LOCALITY. Morelet (1860) lists it as, 'Habitat, rara, in sylvis Guinea.' His two syntypes in BMNH were more specifically labeled 'Gabon,' which is included in the early broad generic geographic term 'Guinea.'

DISTRIBUTION. Sowerby (1890) described *Achatina barriana*

Table 3 *L. mollicella* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Width	% whorl	% LW/L	% W/L	
6¼	39.8	18.7	17.5	9.3	27.7	70	47	Bitya (BMNH) Para <i>L. m. zenkeri</i> 1908.6.3.2
6½	37.5	17.7	17.3	8.9	26.5	71	47	Ebalowa (UMMZ)
6¼	35.8	17.5	18.4	8.7	26.5	74	49	Yaoundé (UMMZ)
6½	33.3	17.3	15.9	10.3	23.4	70	52	Olounou (MRAC) 796.850
6	30.5	16.1	15.6	8.2	22.3	73	53	Kribi (MRAC) 795.638†
6	30.0	14.8	15.0	7.5	21.4	71	50	Calabar (BMNH) Holo <i>A. smithi</i>
6	26.7	13.4	12.8	6.2	18.9	71	50	Gabon (BMNH) Lect. <i>A. mollicella</i> *
6	26.6	14.0	13.6	6.9	19.1	72	53	93.2.4.119 Bonjongo (MRAC) 5315 PLec <i>A. pulchella</i>
5½	23.6	13.1	12.4	6.6	17.3	73	55	Gabon (BMNH) PLec <i>A. mollicella</i> 93.2.4.120
4¾	16.6	10.4	9.1	5.0	12.2	73	63	Nyong (ZMUC)†

Total specimens examined: 35. Sources: BMNH, IRSN, MNHN, MRAC, NHMW, NMW, SMNH, UMMZ, ZMUC.

and *A. smithi* (= *L. mollicella*) at the same time and indicated for both that the locality was 'Calabar, Africa?' (4° 57' N, 8° 19' E). Both specimens were from the Cuming collection, in which a number of other locality records from time to time have been questioned or proven incorrect. J.C. Reid of the University of Calabar has collected near Calabar what is now confirmed as *Callistoplepa barriana*, but so far no *L. mollicella*. It is altogether possible that this latter species eventually will be found in Nigeria because Mbonge, Cameroon, a known endemic locality for this species, is only ca. 70 km to the southeast in a similar environment. Ortiz & Ortiz (1959:26) have reported the western-most records for this species from four localities on Fernando Póo Island (= Macias Nguema Biyogo) of Equatorial Guinea 3° 30' N, 8° 40' E. Seventeen locality records on the continent cluster in the northwestern corner of Cameroon, with the extremes being Mbonge 4° 33' N, 9° 05' E in the North, Molobo 4° 01' N, 14° 19' E in the East, and Efulen 2° 42' N, 10° 30' E in the South. Vignon through Ancy (1888:70) records this species as being very rare in the forests of Gabon. It probably is not found south of the Ogooué River.

In the specimens examined, there was a high direct correla-

tion between greater shell size and distance from the sea-coast, e.g. the largest specimen seen in this study is from Bitya on the river Dja, ca. 260 km from the coast 3° 01' N, 12° 22' E (BMNH no.1908.6.3.2; Table 3).

Leptocala petitia (Jousseaume, 1884)

Figs. 29, 30

Petitia petitia

Jousseaume, 1884:172, pl. 4, fig. 4a, holotype, monotypy (*non* Chitty, 1857); Bequaert, 1950:138.

Achatina (Leptocala) mollicella petitia

Pilsbry, 1904:73, pl. 34, fig. 15 (ex Jousseaume, 1884); Bequaert, 1950:138, pl. 58, fig. 4.

Leptocala mollicella petitia

Bequaert & Clench, 1934b:273.

SHELL. Shell ovate-elongate, thin but not fragile; last whorl shiny, upper whorls less so. Whorls 6½–7, moderately convex. Spire slender conic; apex narrowly obtuse; sutures fine, almost without irregularities. Last whorl expanding proportionately to upper whorls, 70% of shell length (n=7); fourth and fifth whorls subcarinate. Aperture elongate-oval, milky within. Columella short, straight, transversely to obliquely truncate. Outer lip thin, arcuate, joining the periphery at an acute angle. Parietal callus minutely granular, shiny, concolorous.

Shell ground colour is pale corneous. At the junction of the fifth and sixth whorls, diffuse yellow-brown stripes (0.3–0.5 mm wide) alternate with wide ground colour bands (0.5–0.7 mm); these are approximately the same width on the early whorls, but become slightly or much narrower, more distinct and closer together on the last whorl, or nearly disappear; they may be variously straight, diagonal or rippled.

The last quarter of the first whorl has nearly imperceptible surface irregularities that originate close to the suture, where they evolve into a series of closely packed crescentic lines. They quickly multiply axially into five or six horizontal series of short crescentic lines. These gradually fuse vertically to form very narrow, crowded, thread-like, prosocline welts. A fairly conspicuous diagonal line, near mid third whorl, marks the end of the nepionic whorls. Near there, the welts become superficially engraved with a vertically oriented, exceedingly fine vermiculate-granulate sculpture, which is reminiscent of the much coarser sculpture of *Achatina (Tripachatina) vignoniana* Morelet, 1874. Gradually, the welts diminish and the more sparse growth lines emerge, leaving the rash-like microscopic sculpture to dominate. This is best seen in subdued light at a low angle. The sculpture may diminish and become more sparse between the third and fourth whorls, as it does in the holotype, or it may continue at essentially the same caliber until the fourth or fifth whorl. At a certain point in the diminution, and if the light intensity is properly adjusted, ghost-like, engraved spiral lines, here and there, spaced as in *L. mollicella*, can be distinguished, especially below the periphery, where the sculpture is somewhat reduced in calibre. The sculpture may extensively obscure these spiral lines and all but traces of a rhomboid pattern, or it may become so sparse on the lower whorls as to allow the sharp spiral lines to dominate. It is almost as if the vermiculate-granulate sculpture were superimposed upon the typical sculpture of *L. mollicella* in a variably decreasing intensity from apex to base. As a result, the surface of the

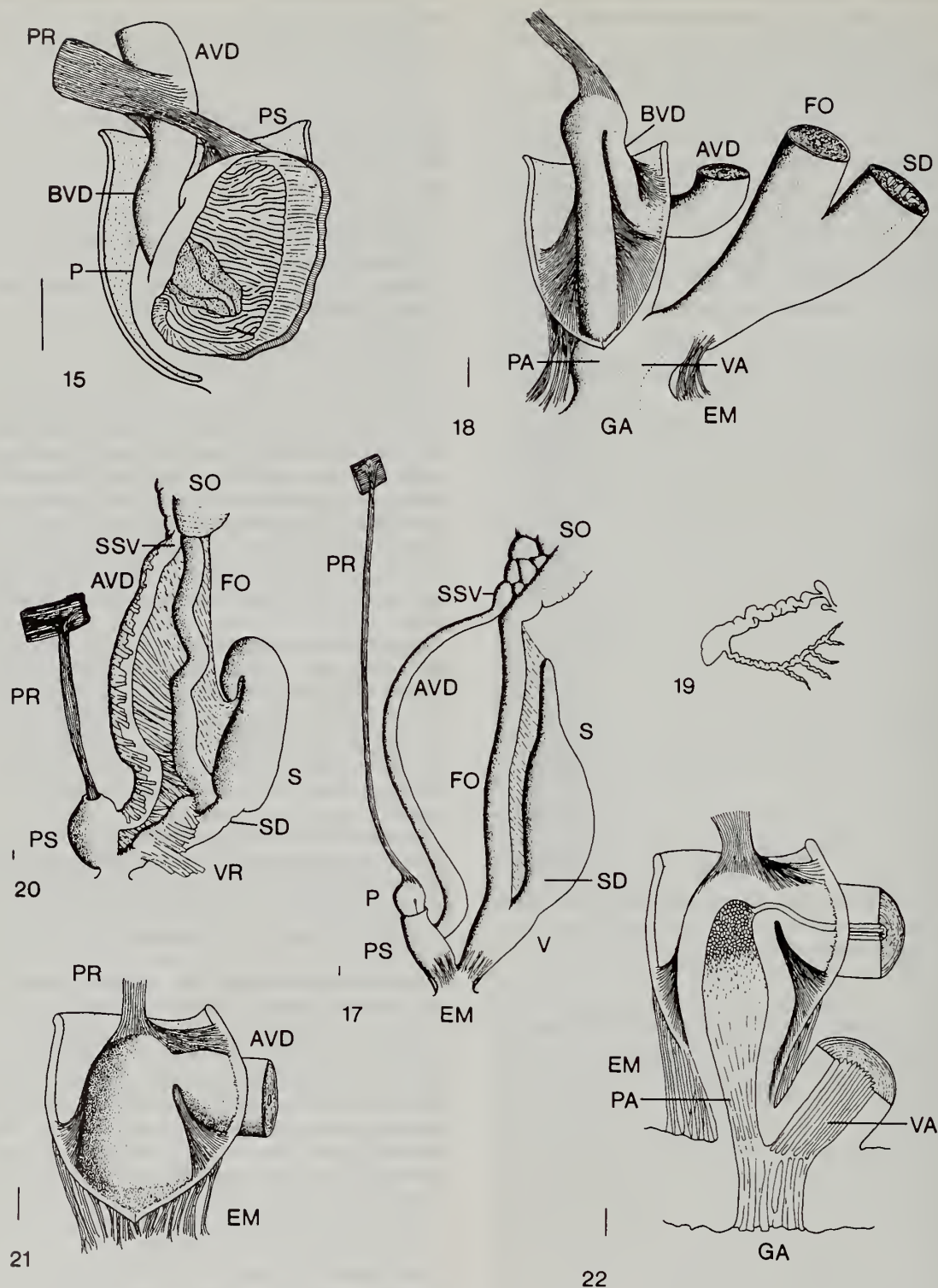


Fig. 15 *L. petitia*, penis sheath and penial wall cut diagonally in right ventrolateral view and spread to expose the pilaster. The cutaway shows the basal vas deferens joining the aperture of the pilaster (MRAC no. 214.044 & 212.583).

Fig. 17 *Bequaertina pinto*, basal genital structures (NM).

Fig. 18 *B. pinto*, penis sheath cut and spread laterally. Conduits transected. Most of the obscuring basal eversion muscle bands have been removed.

Fig. 19 *B. pinto*, hermaphroditic duct system.

Fig. 20 *Bequaertina graueri*, basal genital structures (MRAC no. 610.342 & 610.303).

Fig. 21 *B. graueri*, penis sheath cut and spread.

Fig. 22 *B. graueri*, frontal plane through basal male and female conduits. Bar scale = ~ 1 mm. A.R.M. del.

shell has less luster than in this latter species. This peculiar microscopic sculpture on the upper whorls is determinative.

SOFT ANATOMY. Alcohol preserved specimens available 2/dissected 2. Congo Republic: MRAC 1/1; Zaire: MRAC 1/1. These apparently are the only such specimens extant. Both had small body masses and were withdrawn far into their thin shells because they were collected during the dry season and were inadequately drowned before preservation. However, most of the soft parts were successfully extracted with only minimal damage to one shell.

Body colour and texture as in *L. mollicella*.

Upon exposing the reproductive tract (Fig. 14), the most noticeable anatomical feature is that both the unusual hull-shaped penis (P) and the large basal vas deferens (BVD) show through the thin, nearly transparent, but substantial, penis sheath (PS). Typical of the Callistoplepinae, the PS also enshrouds the very short penial retractor (PR). As in *L. mollicella* and *Callistoplepa barriana*, this latter inserts far posterior on the large right columellar retractor (RCR). Also conspicuous is the apparently inordinately long bipartite apical vas deferens (AVD), with a nearly evenly broad muscular basal portion and a thin-walled, somewhat undulant apical portion. When the PS was cut vertically and the edges pulled laterally, it was found to extend essentially to the base of the P. In the first dissected specimen, from Lukula, Zaire, the exposed, large BVD appeared out of proportion and excessively deeply wedged into the ventral surface of the P. Similarly, the navicular P, with its diagonal left ventrolateral orientation, seemed enigmatically distorted. But the second specimen, from Kayes, Congo Republic, ca. 180 km to the north, had almost identical proportions and alignment, thus essentially removing the suspicion that there had been excessive distortion. The relatively thin penial wall of the first specimen was cut along a midventral, vertical line. Immediately below the surface was a large, obstructing mass of penial wall tissue whose angulate orientation could not safely be explored. Consequently, in the second specimen, a diagonal cut was made along the long axis of the oblong P. This revealed in right ventrolateral aspect a comparatively huge, somewhat compressed potato-shaped pilaster (PIL) attached diagonally along nearly its full length ventrolaterally on the inner basal penial wall, parallel to the adjacent crowded BVD (Fig. 15). In essence, the wall of the basal half of the P was hardly more than a thin, tight-fitting cover for the PIL. The surface of the PIL and the inner wall of the P, similar to that of *L. mollicella*, was covered with transverse, diagonal, anastomosing rugae. Irregularities in the rugae revealed a small basal aperture. Cutting basally into the 2.6 mm PIL exposed the short basal-most BVD narrowing rapidly through dense connective tissue to connect with this aperture. Apically, the PIL is a solid mass of penial wall tissue. Collectively, the relationships in these structures are reminiscent of those in *C. shuttleworthi*, particularly with respect to the exposed BVD pushing ventrally far down into the partially evaginated P (Figs. 4, 5).

In this species the basal female conduit, externally and internally, is much less gross than in *L. mollicella*. The vagina (V) is a distinguishable, more slender portion of the conduit. Similarly, the basal spermathecal duct (SD) is less muscular and tends less to interject itself between PS and the free oviduct (FO). However, the FO, muscular at the base and thin-walled apically, is less robust yet comparatively more prominent in this species. Although shown spread apart in

Fig. 14 for clarity, the FO and basal SD are actually held tightly together by many small, short muscle bands, probably providing support for the SD at termination of copulation. In that natural position, the clavate spermatheca (S) is attached by thin muscle bands and connective tissue to the uterine portion of the spermoviduct, well above the junction of AVD and FO. The eggs are not known but are probably on a par with those of *L. mollicella*.

TYPE MATERIAL. The holotype (monotypy) (Figs. 29, 30; Table 4) in the Jousseume collection in Paris (MNHN) was collected by L. Petit.

TYPE LOCALITY. At the mouth of the River N'toc, which disappears in the Mayumba Lagoon, Gabon 3° 25' S, 10° 39' E.

DISTRIBUTION. Gabon: type locality. Congo Republic: Sibiti 3° 41' S, 13° 21' E (SMNH), Kola 4° 03' S 11° 44' E (MRAC), Kayes 4° 26' S, 11° 23' E (MRAC). Zaire: Lukula 5° 21' S, 13° 02' E (MRAC). All known localities are south of the Ogooué River of Gabon. This species will probably be found in Cabinda, Angola.

REMARKS. In addition to the holotype in Paris (MNHN), there are only six known specimens of this species, five in Tervuren (MRAC), collected by Darteville, and a single specimen in Stockholm (SMNH). The explanation for its apparent rarity probably rests in the fact that there has been much less professional collecting in south coastal Gabon and the Congo Republic than in Cameroon, where *L. mollicella* is not a rarity. In this limited number of specimens extant, there is a north to south gradient of more intense vermiculate-granulate sculpture and reduced rhomboid pattern. If the substantive differences in the soft anatomies had not been known, this taxon might well have been assumed to be no

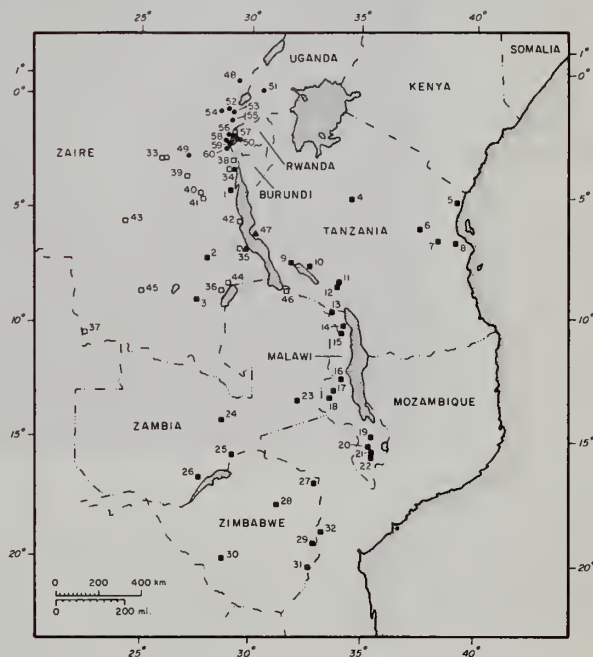


Fig. 16 Distribution of *Bequaertina*. ○ = *Bequaertina fraterculus*, ● = *B. graueri*, □ = *B. pellucida*, ■ = *B. pintoi*, ▲ = *B. marteli*. Where possible, all localities were checked with the volumes of the U.S. Board on Geographic Names.

Table 4 *L. petitia* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Width	% whorl	% LW/L	% W/L
7	32.5	14.8	14.3	7.5	21.5	66	45 N'toc (MNHN) Holo *
6½	30.9	14.2	14.5	7.1	21.4	69	46 Sibiti (SMNH)
6¼	30.8	14.8	13.9	7.2	21.3	69	48 Lukula (MRAC) 212.583†
6½	29.0	13.7	14.0	6.5	20.1	69	47 Kola (MRAC) 196.340
6	28.6	14.6	14.5	7.1	20.5	72	51 Kola (MRAC) 196.341
6	23.9	12.3	11.6	6.0	16.4	69	51 Kayes (MRAC) 214.004†
5	20.8	13.3	11.8	6.3	15.1	72	64 Kola (MRAC) 791.389

Total specimens examined: 7. Sources: MNHN, MRAC, SMNH.

more than a subspecies of *L. mollicella*, as Bequaert & Clench concluded (1934b:273). This case is reminiscent of the conchologically very similar but anatomically contrasting *Achatina reticulata* Pfeiffer, 1845 and *A. albopicta* E.A. Smith, 1878 (Mead, 1950:232).

Jousseume's illustration of the holotype is misleading because the artist has shown the apex acuminate; actually, the first and second whorls are noticeably larger, producing a narrowly obtuse apex.

Apparently neither Leonardo Fea (Germain, 1916) nor Captain Vignon (Ancey, 1888) went far enough south in Gabon to encounter true *L. petitia*.

ACHATININAE

Bequaertina new genus

Thin, fragile, anomphalous, medium to large, ovate to ovate-elongate shells, 40–80 mm in length. Spire tends to be mammillate, apex obtuse. Aperture large, columella long and slender, squarely or obliquely truncated. Whorls 6–6½, rarely 7; second and third nepionic whorls sculptured; last whorl ventricose, ca. 80% of shell length. Sculpture may be variously cancellate-granulate, lirate, malleate or nearly smooth. Surface of shell lusterless; its abrasion reveals a brilliant inner periostracal layer. An occasional specimen may show in the periostracum of the lower whorls limited areas of an extremely fine decussate micromesh, commonly seen in a wide variety of achatinids.

The generic characters in the soft anatomy are based on features that are shared by the two available species – *B. pinto* (Bourguignat, 1889) and *B. graueri* (Thiele, 1911). Because of the similarity in the basic anatomical pattern in these two species, and because, on the basis of shell characters, each of the species represents a different dichotomous group, it is felt that the following anatomical characters will prove to be valid for the genus.

The most prominent features of the genital system are the long free oviduct, the apical vas deferens and the large,

elongate sacculate spermatheca – all held in close juxtaposition by a distinct fascia. In contrast, the penis and penis sheath are inconspicuous. The penis sheath enshrouds a short basal portion of the long vas deferens. Without exception in 26 dissected specimens, the penial retractor inserts on or near the diaphragm where the latter joins the mantle and the body wall of the neck region. At the origin of the penial retractor, muscle fibrils pass snugly over the apical penis and then fan out into a network that covers the basal vas deferens and the inner wall of the penis sheath, except for a limited smooth, shiny zone on the approximately upper half of the left side. Below this, the fibrils infuse intimately with the tissues of the basal penis and penis sheath to create an ill defined section of the male conduit that contains the penial atrium. This atrium connects the lumen of the penis with the genital atrium. At this level, abundant hypertrophied eversion muscle bands obscure the genital atrium and its junction with the male and female conduits. There is no pilaster or verge.

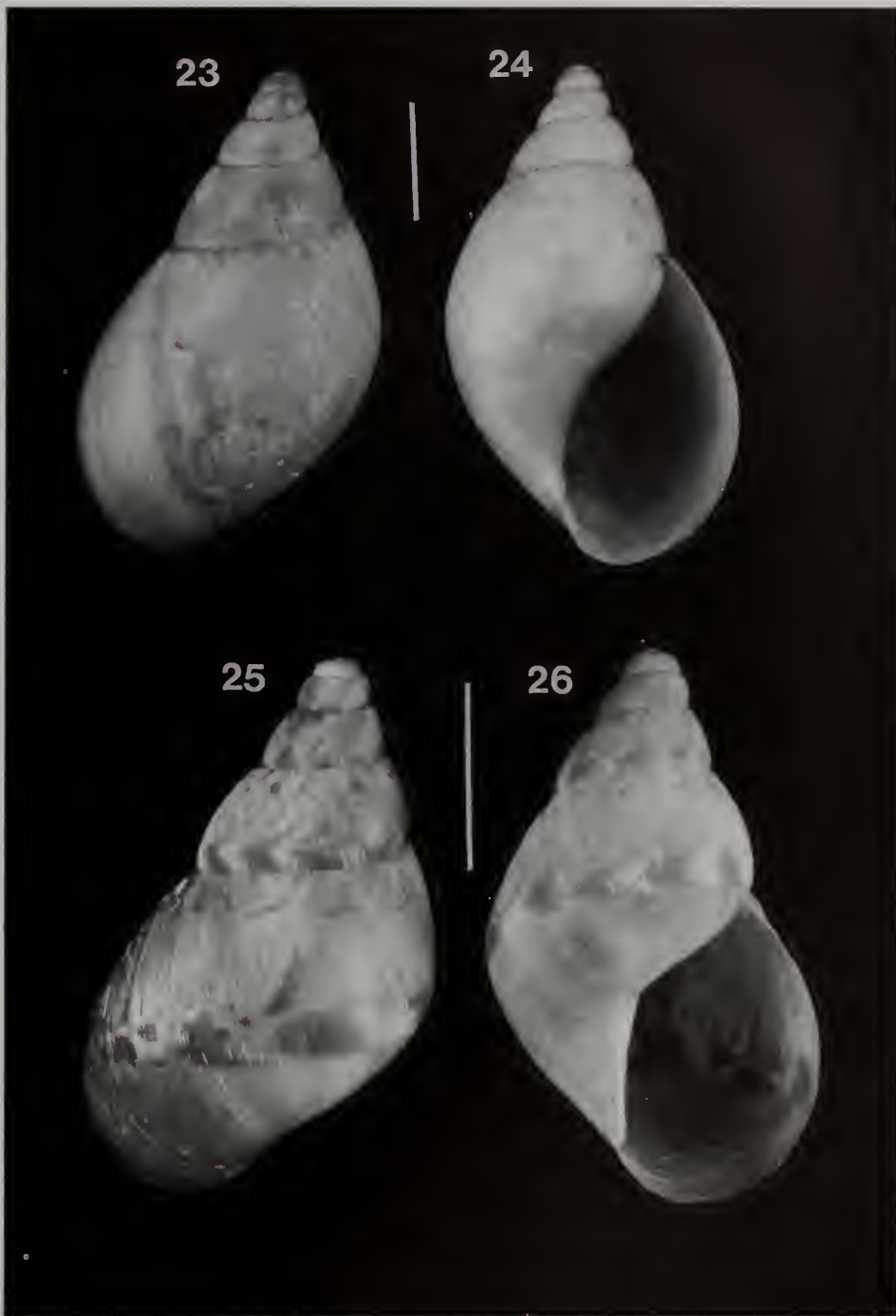
The spermathecal duct is much shorter than the spermatheca and often sessile on the vagina. This significantly places the spermatheca in a basal position with its usually attenuated apex stretching to its connection by fascia to the junction of the free oviduct and the apical vas deferens, well below the spermoviduct. The hermaphroditic duct has in its midsection an enlarged glandular structure of unknown function. The ductules to the five hermaphroditic acini are inordinately gross and highly convoluted.

The eggs are covered with a hard calcareous shell and are proportionately larger than those of *Achatina*, i.e. on a par with those of *Tholachatina* (*sensu* Bequaert, 1950). There is no evidence of ovoviviparity.

The anterior aorta is on the floor of the diaphragm and passes ventrally through the diaphragm to the sagittal myoseptum in the haemocoel. The second largest vein in the lung drains the region near the extreme left mantle and joins the primary vein near the apex of the kidney. The large last whorl of the shell allows for a highly vascularized left side of the lung. The secondary ureter is completely closed. The rachidian tooth of the radula is either slender and questionably functional or broad and about half the size of the adjacent laterals. The jaw is narrow and broadly arcuate, with many slender vertical ribs irregularly distributed.

Six specimens of *B. pellucida* (Putzeys, 1898) and one of *B. marteli* (Dautzenberg, 1901), as well as several of *Achatina craveni*, have been found with a single, almost perfectly circular hole, 0.6–4.0 mm in diameter, cut usually in the dorsal part of the last whorl. These are thought to be caused by bird pecks (Meredith, 1983a:25).

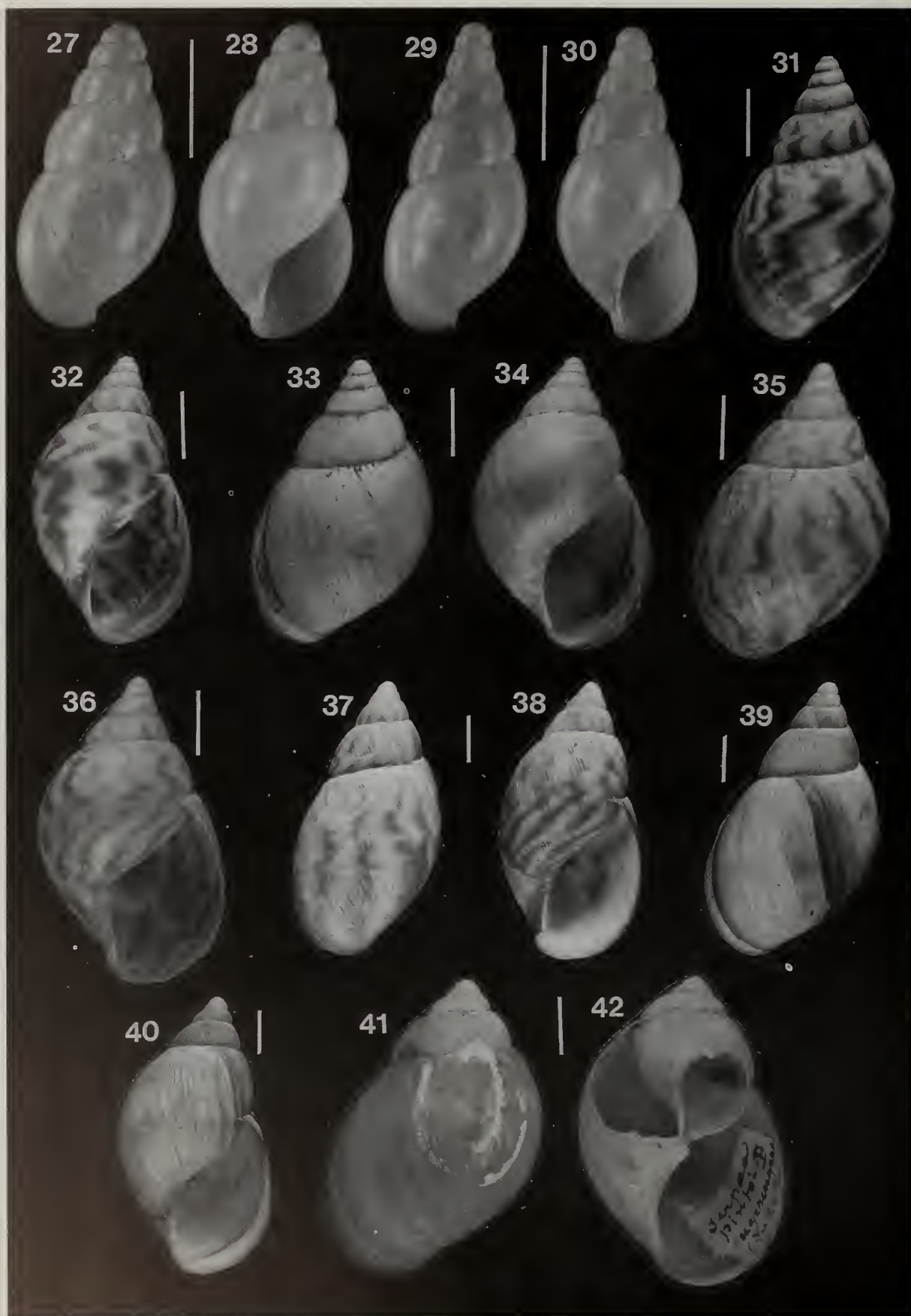
The five species in this genus were placed in the genus *Callistoplepa* on the basis of similar shell characters: thin shell, large aperture and a tendency to form a mammillate spire (Pilsbry 1919, Bequaert & Clench 1934c). But as shown in the Key to Subfamilies, a study of the internal anatomies revealed major differences. *Bequaertina* reflects strongest phylogenetic affinities to subgenus *Achatina* (*sensu* Bequaert, 1950), particularly with respect to the configuration of the basal male conduit and to the fact that the spermatheca is attached to the adjacent free oviduct and apical vas deferens rather than to the spermoviduct. In *Bequaertina*, the apical penis is free from the apical penis sheath and therefore can evert independently, with the sheath following seriatim at extroversion, whereas in subgenus *Achatina* the penis is completely enmeshed in a dense network of muscle fibrils and connective tissue that requires the penis and the sheath to

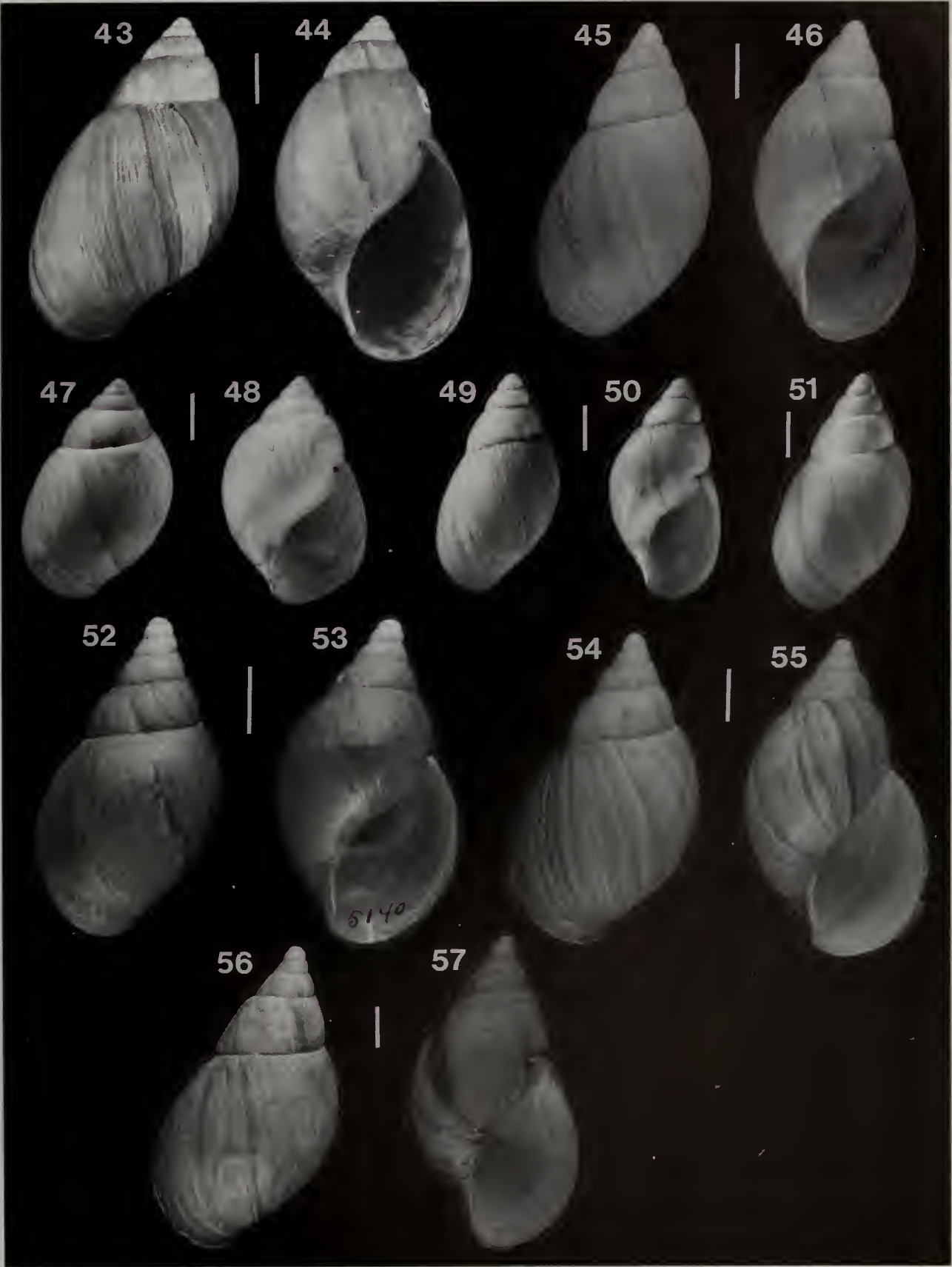


Figs 23, 24 *Callistoplepa barriana* (Sowerby, 1890); lectotype *Achatina barriana* BMNH no. 1889.11.19.2. **25, 26** *C. shuttleworthi* (Pfeiffer, 1856); lectotype *Achatina shuttleworthi* BMNH. Bar scale = ~ 10 mm.

Figs 27, 28 *Leptocala mollicella* (Morelet, 1860); lectotype *Achatina mollicella* BMNH no. 93.2.4.119. **29, 30** *L. petitii* (Jousseaume, 1884); holotype *Petitii petitii* MNHN. **31, 32** *Bequertina pellucida* (Putzeys, 1898); lectotype *Ganomidos pellucidus* MRAC no. 5135. **33, 34** *B. pellucida*; paralectotype *G. pellucidus* (unicolorous) MRAC no. 5136. **35, 36** *B. pellucida*; lectotype *Serpaea foai* Germain, 1905 MNHN. **37, 38** *B. marteli* (Dautzenberg, 1901); lectotype *Achatina marteli* IRSN. **39, 40** *B. marteli*; lectotype *A. marteli pallescens* (Dautzenberg, 1901) IRSN. **41, 42** *B. pintoii* (Bourguignat, 1889); holotype, *Serpaea pintoii* MNHN. Bar scale = ~ 10 mm.

Figs 43, 44 *B. pintoii*; lectotype *Achatina fragilis* Smith, 1899 BMNH no. 97.12.31.9. **45, 46** *B. pintoii*; holotype, *Callistoplepa thielei*, Bequaert & Clench, 1934c ZMB no. 53177. **47, 48** *B. pintoii*; BMNH no. 1885.5.25.47. **49, 50** *B. pintoii*; BMNH MacAndrew (1563). **51** *B. pintoii*; BMNH no. 1907.7.25.3. **52, 53** *B. fraterculus* (Dupuis & Putzeys, 1900); lectotype *Ganomidos fraterculus* MRAC no. 5140. **54, 55** *B. graueri* (Thiele, 1911); lectotype *Achatina graueri* ZMB no. 101935. **56, 57** *B. graueri*; lectotype *Callistoplepa babaulti*, Germain, 1936 MNHN. Bar scale = ~ 10 mm.





evert together as a unit, forming a quite different intromittent organ. The very shell characters that seemed to link these five species with *Callistoplepa* now are seen conchologically to distinguish the more primitive genus *Bequaertina* from *Achatina* s.s.

On the basis of somewhat overlapping shell characters, available distributional records, and the limited anatomical evidence, the species of *Bequaertina* break into two groups: (1) the malleate, mammillate *B. fraterculus* (Dupuis & Putzeys, 1900) and *B. graueri*, and (2) the cancellate *B. pellucida*, *B. marteli* and *B. pintoii*. *B. pellucida* of southeast Zaire, close to what is believed to be its ancestral home, is plesiomorphic within the group and stands between an ancestral achatinid stock of the Zaire Basin and *Achatina* s.s., which today is largely restricted to that basin. A branch of the ancestral stock moved north and northeast to give rise to the apomorphic *B. fraterculus* and *B. graueri*. A more conservative second branch moved east to give rise to *B. pellucida* and *B. marteli*. This second branch continued further east and then into a strong north-south axis to give rise to the closely related *B. pintoii*. The known distribution of the genus (Fig. 16) embraces a vast area of the Rift Valley – Lake Region and the Lualaba branch of the Zaire River in central, eastern and southeastern Africa. Greater field collecting will probably extend the limited distributions of *B. fraterculus* and *B. marteli*.

Pilsbry & Cockerell (1933), on the erroneous assumption that *Achatina graueri* 'represented an intrusion of a South African type into the Central African region', initially decided to place it in the genus *Cochlitoma*. They softened their stand on the advice of M. Connolly and designated it '*Achatina (Cochlitoma) graueri*'. However, this species cannot possibly be considered congeneric with *Cochlitoma zebra* (Bruguère, 1789), which Pilsbry (1904:xiii, 78) selected as the type species of the genus *Cochlitoma*, because Mead (1992) shows *Achatina zebra* anatomically belongs to subgenus *Tholachatina* of *Archachatina*. Since the present group of five species is not congeneric with the species in either *Callistoplepa* or *Achatina* s.s., and since this group also is not congeneric with *Achatina hortensiae* Morelet, 1866, which Pilsbry (1904:21) selected as the 'type' of *Serpaea*, there is no other available genus-group name. *Ganomidos* cannot be considered because it is a junior subjective synonym of *Callistoplepa*. For these reasons, the generic name *Bequaertina* is proposed. It is named in honour of the late Dr Joseph C. Bequaert, Agassiz Professor of Zoology at Harvard University, who will remain the classical authority not only in the Achatinidae, but also in several families of insects and arachnids that he mastered in his long lifetime. Because *B. graueri* is the largest and most conspicuous of the five species, and because it has departed farthest from what is believed to be the ancestral stock, it is here selected as type species of the genus.

Early in the present study, it became obvious that this group of five species anatomically was not congeneric with *Callistoplepa*. This information was shared with colleagues who considerately referred to this new genus in general terms (van Bruggen, 1978:912, 921, 1988:10; van Bruggen & Meredith, 1984:161). Also, the present author made reference to this new genus in an earlier manuscript as '*Callistoplepa* s.l.' (Mead, 1992).

Key to Species

- 1 Last whorl distinctly granulate above the periphery, or at least in a limited subsutural zone; growth wrinkles conspicuous to dominant 2
- Last whorl faintly granulate, malleate, lirate or smooth except for modest irregular growth wrinkles 4
- 2 Apex broadly obtuse; 6 whorls = > 50 mm; yellowish, ochraceous or olivaceous; gross granulate sculpture; first nepionic whorl 2–3 mm in diameter; second whorl expanding broadly; sculpture of second whorl coarse and either distinctly granular or depressed and poorly defined; transverse measurement at junction of third and fourth whorls is 2½–4 mm; outer lip increasingly arcuate basally; growth wrinkles bold or moderately heavy 3
- Apex subacute to narrowly obtuse; 6 whorls = ~ 40 mm, 7 whorls = 53–60 mm; translucent dull fulvous to dull olivaceous-brown; moderately coarse to fine granulate sculpture; first nepionic whorl 2 mm in diameter; second whorl tends to be slightly constricted, expanding limitedly; sculpture of second whorl finely engraved, delicate; transverse measurement at junction of third and fourth whorls is 2–2½ mm; outer lip evenly arcuate; growth wrinkles thin, of modest calibre. Southeast Zaire, northeast Zambia and west central Tanzania *pellucida*
- 3 Last whorl large, rarely strikingly so; ground colour intense olivaceous-yellow to subdued olivaceous; prominent closely aligned somewhat irregular costate transverse ridges embrace the gross elongate granules with bold vertical emphasis, dominating the spiral lines; strongly contrasting zigzag castaneous flammules usually present, pale unicolorous forms uncommon; first nepionic whorl 2½–3 mm in diameter; sculpture of second whorl coarse, granular, elevated, tightly packed; transverse measurement at junction of third and fourth whorls is 3–4 mm; third whorl deeply and grossly granulate. Middle west and east shores of Lake Tanganyika, Zaire and Tanzania *marteli*
- Last whorl large, often very large to ventricose; ground colour dark olivaceous to pale olivaceous yellow; coarse granulate sculpture above periphery, reduced or absent below periphery (varies within a single whorl); transverse ridges moderate, slender, fairly uniform, in balance with the spiral lines, conspicuous below periphery but obscured by granulate sculpture above periphery; usually unicolorous, but narrow fairly straight light castaneous stripes may be present; first nepionic whorl 2–2½ mm in diameter; sculpture of second whorl coarse, but superficial, vaguely and irregularly impressed, patchy, poorly defined, often worn smooth; transverse measurement at junction of third and fourth whorls is 2½–3 mm; third whorl delicately to moderately granulate. East Africa, almost reaching the Limpopo River in the south (4–20° S, 27–39° E) *pintoii*
- 4 Apex of shell obtuse and noticeably mammillate; shell conspicuously to obscurely malleate; opaque or dark and translucent, uniformly or somewhat variably brown or yellow-brown, banding limited and irregular; coarse growth wrinkles or extremely fine lirae dominate the sculpture, 6 whorls = > 43 mm 5
- Apex of shell subacute to narrowly obtuse, somewhat elevated but not mammillate; shell not malleate; translucent dull fulvous to dull olivaceous-brown, usually with moderately broad castaneous flames and stripes irregularly distributed, but may be pale unicolorous; very fine granulate-cancellate sculpture dominates; 6 whorls = < 43 mm. Southeast Zaire, northeast Zambia and west central Tanzania *pellucida*
- 5 Shell large (6¼ whorls = 60–80 mm), thin but substantial, essentially opaque; usually conspicuously malleate; not carinate; growth wrinkles prominent, rather regular; lirae of fifth whorl distinctly transacted by spiral striae; unicolorous or

Table 5 Locality records – *Bequaertina*. Numbers in the first column correspond to the locality numbers in Figure 16. Sources of specimen information are shown in the last column.

1. Lake Tanganyika, 1800–2000m	4° 30' S, 29° 00' E	NHMH [†]
2. Kiambi	7° 20' S, 28° 01' E	Dautz. & Germ., 1914
3. Sampwe (<i>non</i> 'Sangue')	9° 20' S, 27° 26' E	Dautz. & Germ., 1914
4. Ibahi, Ugogo (=Ougogo) Riv.	5° 04' S, 34° 04' E	Ancey, 1902
5. Mbwe (=Mbwego)	5° 21' S, 38° 58' E	Ancey, 1902
6. Mamboya (=Mambo)	6° 16' S, 37° 06' E	BMNH
7. Morogoro	6° 50' S, 37° 45' E	BMNH
8. Ngerengere, Oukani, Kingoni	7° 03' S, 38° 31' E	Bourg., 1889
9. Ufipa (=Sumbawanga)	8° 00' S, 31° 30' E	Ancey, 1902
10. Rukwa Lk.	8° 00' S, 32° 25' E	BMNH [†]
11. Mbaya, 1700m	8° 45' S, 33° 27' E	BMNH, LNK
12. Utengule	8° 54' S, 33° 20' E	BMNH, MCZ, ZMB, SMF
13. Misuku Hills, Mughoma, 1500m	9° 40' S, 33° 33' E	RMNH [†]
14. Deep Bay (=Chilumba, =Hengwa)	10° 27' S, 34° 16' E	BMNH
15. Nyika Plateau, 6000–7000 ft.	10° 48' S, 33° 48' E	BMNH, IRSN, MCZ et al.
16. Nkota-Kota	12° 55' S, 34° 18' E	BMNH
17. Nchisi (=Ntchisi) Mt.	13° 20' S, 34° 05' E	HM [†]
18. Chinyama	13° 43' S, 33° 43' E	HM [†]
19. Zomba, Shirwa Lk., Mpita	15° 23' S, 35° 23' E	BMNH, IRSN, RMNH
20. Chiradzulu Mt., Lisau	15° 41' S, 35° 09' E	HM [†]
21. Nyambadwe Hill	15° 48' S, 35° 15' E	NG [†]
22. Soche Mt.	15° 51' S, 35° 01' E	NG [†]
23. Cheri Bridge, Upper Lauangwa	13° 35' S, 31° 30' E	MCZ
24. Broken Hill (=Kabwe)	14° 27' S, 28° 27' E	NMW
25. Kafue Riv., Mumbwa	15° 56' S, 28° 55' E	Beq. & Cl., 1934c
26. Pemba	16° 40' S, 27° 25' E	SAM
27. Mazoe Valley	16° 32' S, 33° 25' E	NMW
28. Salisbury	17° 50' S, 31° 03' E	NM
29. Vumba, Zonwi Bridge, 2500 ft.	19° 07' S, 33° 05' E	NM [†]
30. Bulawayo	20° 09' S, 28° 35' E	RMS, SAM
31. Chirinda, Selinda Mt., 4000 ft.	20° 26' S, 32° 42' E	BMNH, MCZ
32. Macequece, Vila de Manica	18° 56' S, 32° 53' E	BMNH, NMW, SAM
33. Nsendwe, Maniema	2° 57' S, 25° 56' E	BMNH, MRAC
34. Uvira	3° 24' S, 29° 08' E	ZMB
35. Mpala (=Pala)	6° 45' S, 29° 31' E	IRSN
36. Mweru (=Moero) Lk.	9° 00' S, 28° 45' E	BMNH, IRSN
37. Dilolo	10° 42' S, 22° 20' E	SMF
38. Rumonge	3° 11' S, 29° 08' E	MRAC
39. Kapuri (=Piani Kapuri)	3° 34' S, 26° 53' E	BMNH, IRSN, MRAC et al.
40. Luaye	4° 42' S, 27° 23' E	MRAC

variably transversely striated with yellow-brown to dark brown; nepionic whorls densely granulate. Lake Kivu district of Zaire, Rwanda, Uganda *graueri*

- Shell small (6¼ whorls = ~ 50 mm), extremely thin, fragile, translucent; malleations very shallow, often sparse; subcarinate at periphery, producing a bend in the arc of fine prosocline lirae; lirae of fifth whorl not transacted; ground colour dull dark brown-olive with irregular castaneous brush marks that are closely highlighted aperturally with buff; nepionic whorls faintly granulate. Lualaba River, Zaire *fraterculus*

Bequaertina pellucida (Putzeys, 1898)

Figs. 31–36

Ganomidos pellucidus

Putzeys, 1898:84, text fig. 20, 21.

Callistoplepa pellucida

Pilsbry, 1905:128, pl. 43, fig. 3, 4; Germain, 1909:90; Pilsbry, 1919:81; Bequaert & Clench, 1934c:114; Haas, 1936:13.

Serpaea foai

Germain, 1905:255; 1908:631.

Achatina foai

Verdcourt, 1966:111; 1983:219.

Callistopepla pellucida

Oliver, 1983:9.

SHELL. Shell ovate-achatiniform to elongate-ovate, extremely thin, very fragile, translucent. Whorls 6–7, rarely 7½; a conspicuous demarcation at or near the end of the third whorl sets off the nepionic whorls. Spire conic, with a narrowly obtuse apex that is slightly elevated; occasionally the second nepionic whorl is somewhat constricted, producing a submammillate profile. Whorls slightly convex, expanding and descending proportionately. Sutures moderately deep

Table 5 continued

41. Kabambare	4° 42' S, 27° 43' E	ZMB
42. Lukuga Riv. mouth	5° 55' S, 29° 12' E	MCZ
43. Gandajika	6° 45' S, 23° 57' E	MRAC
44. Pweto	8° 26' S, 28° 55' E	IRSN
45. Kamina	8° 44' S, 25° 00' E	MRAC
46. Abercorn (=Mbala)	8° 50' S, 31° 22' E	MCZ
47. Kungwe, Sitete (=Nkungwe)	6° 07' S, 29° 48' E	Verdcourt, 1966
48. Beni	0° 30' N, 29° 28' E	IRSN, MRAC
49. Kitembo	2° 53' S, 27° 37' E	MNH
50. Lobengera Mission	2° 03' S, 29° 25' E	MRAC
51. Ibanda	0° 08' S, 30° 30' E	MRAC
52. Loashi Valley	1° 14' S, 28° 45' E	MRAC
53. Burungu, Ruasa	1° 20' S, 29° 02' E	ANSP
54. Nyabukere	1° 29' S, 28° 33' E	MRAC
55. Kirotshe, 1250 m	1° 37' S, 29° 02' E	MRAC
56. Lwiro Riv.	2° 00' S, 28° 52' E	AMNH, FMNH
57. Idjwi (=Kwidschwi, Kwidjwi)	2° 09' S, 29° 04' E	ZMB, MRAC, UMMZ et al.
58. Katana	2° 13' S, 28° 50' E	MRAC
59. Tshibinda	2° 20' S, 28° 45' E	ANSP, MRAC
60. Bukavu	2° 30' S, 28° 52' E	MNH, NMB

[†] = specimens dissected in the present study.

and irregular. Last whorl large, 80% of shell length; range for 5–7½ whorls, 76–84% (n = 52). Aperture oval, faint milky wash within. Columella concolorous, slender, moderately long straight or slightly arcuate and rectangularly to very obliquely truncate. Outer lip extremely thin, evenly arcuate, receding at base in profile. Parietal callus scarcely detectable.

The first two to three whorls are light horn colour. Pale, obscure, castaneous streaks begin to appear in the third or fourth whorl; these characteristically are broader at the suture below, becoming increasingly darker, larger and more irregular on the last whorl. These streaks may be variously vertical, diagonal, angulate, flammulate, interrupted, or reduced to spots and blotches. Ground colour is dull buff to dull olivaceous-fulvous. Of 56 specimens checked precisely for colour, 63% have a definite pattern, 7% are nearly unicolorous, and 30% are unicolorous. There was no correlation between colour pattern and locality.

The first whorl is essentially without sculpture. Minute, faintly engraved crescentic granulations usually appear early in the second whorl; these are formed by nearly equidistant spiral lines and irregular, scalloped transverse lines. The latter become straighter and compressed in the third whorl, producing narrow elongate granulations and irregularly appearing prosocline growth wrinkles that are crenulate at the suture. The sculpture becomes more disperse in the fourth and fifth whorls, producing a dominant, fairly uniform, subquadrate, often welt-like, cancellate-granulate sculpture, which usually fades quickly at the periphery. In the sixth to seventh whorls, this sculpture becomes more and more subdued and diffuse until the increasingly prominent, yet modest, growth wrinkles dominate both above and below the periphery. In the largest specimens of seven whorls the cancellate-granulate sculpture may feebly or strongly return both above and below the periphery. The dull, extremely thin, tenaceous outer periostracal layer wears off in very limited areas, highlighting the sculpture with the exposed glossy inner periostracal layer.

SOFT ANATOMY. No known alcohol preserved specimens.

TYPE MATERIAL. As nearly as can be determined, Putzeys had 14 syntypes of his *Ganomidos pellucidus*, for which he gave a range of shell dimensions (1898). The specimens were collected by P. Dupuis. Putzeys retained a select series of 7 syntypes in his own collection (MRAC no.5132–5138). He did not designate types, but selected the largest specimen (no.5132) for an abaperatural view and a small specimen with slender flames (no.5133) for an aperatural view in his line drawing illustrations. Regrettably, the larger specimen had been rather badly damaged and mended in nature, and the smaller specimen was excessively small. The second largest syntype in his series (no.5136) is a unicolorous specimen that is representative of only about a quarter of the known specimens (Figs. 33, 34). Hence, the flamed, third largest syntype in his series (no.5135) is here selected the lectotype (Figs. 31, 32; Table 6), with the other syntypes becoming paralectotypes (BMNH 1no.1904.5.18.68, IRSN 5, MRAC 6, NHMW 1).

On the basis of two specimens collected by Edouard Foa during his 1897–98 expedition to the Lake District of Africa, Germain described (1905) and figured (1908) the junior subjective synonym *Serpaea foai* from 'Tanganika est', later corrected to 'les bords du Lac Tanganyika'. Bequaert (1950) placed *Serpaea* in the synonymy of *Achatina*, but apparently

Table 6 *B. pellucida* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl % LW/L	% W/L	
7	60.4	31.4	32.7	19.5	45.9	76	52 Mweru (BMNH)
7½	58.6	32.8	36.0	16.6	46.0	79	56 Kamina (MRAC) 581.196
7	54.5	29.0	30.5	17.0	42.5	78	53 Mweru (BMNH) 1907.11.11.5
7	53.3	30.2	31.2	17.8	42.3	79	57 Mpala (IRSN)
6½	48.0	28.0	29.7	15.8	38.0	79	58 Piani Kapuri (MRAC) 5132 PLec
6½	46.9	29.6	29.4	16.5	37.5	80	63 Tanganyika (MNHN) Lect <i>S. foai</i> *
6¼	45.8	28.0	28.0	16.7	37.0	82	61 Piani Kapuri (IRSN) PLec <i>G.p.</i>
6½	45.0	28.2	26.8	15.5	35.5	79	63 Piani Kapuri (MRAC) 5136 PLec <i>G.p.</i> *
6¼	43.2	24.6	25.5	14.1	33.9	78	57 Piani Kapuri (MRAC) 5135 Lect <i>G.p.</i> *
6¼	40.4	22.6	23.0	13.6	31.7	78	56 Piani Kapuri (MRAC) 5133 PLec <i>G.p.</i>
6	39.0	23.3	24.4	14.1	32.0	82	60 Tanganyika (MNHN) PLec <i>S. foai</i>
5¾	35.5	20.0	20.9	12.0	28.4	80	56 PLec <i>G.p.</i> (BMNH) 1904.5.18.68

Total specimens examined: 62. Sources: BMNH, IRSN, MCZ, MNHN, MRAC, NMW, USNM, ZMB.

overlooked Germain's species. Only Verdcourt (1966) has acknowledged the existence of this species, and then only as an East African species unknown to him. A study of the two syntypes in Paris (MNHN) confirmed the fact that they are indeed Putzeys' species. His larger, sharply photographed 'seul adulte' specimen (Figs. 35, 36) is here selected as the lectotype of Germain's *Serpaea foai* (Table 6).

Deshayes (1824–37, 1864) described and illustrated a small fossil snail *Agathina pellucida* (= *Achatina pellucida*) from the Paris basin. Lamarck (1838:313) also refers to this species. This very acuminate, slender specimen is possibly a subulinid. It does not enter into homonymy with Putzeys' *G. pellucidus* because the latter was never included in the genus *Achatina*.

TYPE LOCALITY. Forest of Piani Kapuri, Maniema (=Manyema), Zaire 3° 34' S, 26° 53' E.

DISTRIBUTION. Next to *B. pintoï*, this is the most wide spread species in the genus (Fig. 16). The known specific localities delineate essentially the southeastern quarter of Zaire, with Nsendwe, near Kindu-Port-Empain, Maniema region in the northwest; Uvira, Kivu region in the northeast; Mpala, Tanganyika region in the east; Lake Mwero (=Moero), Kantanga region in the southeast; and Dilolo, Lualaba region in the southwest. The only records outside Zaire are (1) in Abercorn (= Mbala) at the southern tip of Lake Tanganyika, Zambia, and (2) on the Tanzanian east shores of this lake, based on Germain's synonym *Serpaea foai* (1905, 1908). Meredith (1983b) and N. Gray (correspondence) failed to find it during extensive collecting in Malawi. The largest and finest specimens extant were collected in the Lake Mwero region (BMNH) and Kamina (MRAC).

REMARKS. This plesiomorphic wide spread species is most closely related to *B. marteli*. Specimens have been found in mixed lots along with *B. marteli* and *Achatina craveni*. The juvenile specimens of all three species are easily confused. Further, the full grown specimens are quite variable in shape, colour, sculpture and pattern, with the not uncommon atypical forms of each species contributing to the difficulty of identification. The young specimen that Grauer collected in the virgin forest 50 km east of Kasongo, Zaire, and identified as *Achatina fulminatrix* von Martens, 1895 by Thiele (1911:205) was examined in Berlin (ZMB) and found to be *B. pellucida*. Extensive series of this species are in Bruxelles (IRS) and Tervuren (MRAC).

***Bequaertina marteli* (Dautzenberg, 1901)**

Figs. 37–40

Achatina marteli

Dautzenberg, 1901:3.

Ganomidos marteli

Dautzenberg, 1901, pl. 1, fig. 1.

Achatina marteli pallescens

Dautzenberg, 1901:3.

Ganomidos marteli pallescens

Dautzenberg, 1901, pl. 1, fig. 2.

Callistoplepa marteli

Pilsbry, 1905:129, pl. 47, fig. 21 (ex Dautzenberg); Germain, 1909:90; Pilsbry, 1919:81; Bequaert & Clench, 1934c:114.

Callistoplepa marteli var. *pallescens*

Pilsbry, 1905:129, pl. 47, fig. 22 (ex Dautzenberg); Bequaert & Clench, 1934c:114.

'*Achatina* sp. near *tavaresiana*'

Verdcourt, 1966:106, fig. 12; 1988:219.

Callistoplepa marteli

Germain, 1936:151; Oliver, 1983:9.

SHELL. Shell ovate-achatiniform, opaque, thin but not fragile. Whorls 6–6¼, rarely 6½. Spire moderately broad, conic; apex obtuse; only one out of 69 specimens examined had a mammillate apex. Upper whorls only slightly convex, descending proportionately but expanding somewhat more rapidly. Sutures fine and regular in nepionic whorls, shallow to moderately deep and irregular in the following whorls. Last whorl large and more convex, 80% of shell length; range for 4½–6½ whorls, 77–84% (n = 69). Aperture inverted

auriform to ovate-elongate; pale blue-white within; surface pattern and flames show through. Columella straight or weakly arcuate, somewhat slender, concolorous but with a thin calcareous film; usually moderately obliquely truncated. Outer lip thin, extending basally only a slight way below the truncation; its arc is characteristically greatest below midway in the mature specimens. Parietal callus thin but apparent even in the smaller specimens.

The nepionic whorls (first 2½) are unicolorous pale buff-white. This changes imperceptibly to a uniform dull ground colour that varies in specimens from a rather intense olivaceous yellow to subdued olivaceous. In most specimens, faint, very diffuse light castaneous blotches appear in the fourth whorl. At first these are vertical, evenly spaced and broader at their base; but they soon become fragmented apically, darker, and strikingly distorted into diagonal even spiral, irregular streaks, bands and flames that are approximately as wide as the ground colour space between them. In the present study of 69 specimens, 72% are flammate, 13% are vaguely flammate but only on the last whorl, and 15% are without flames, i.e. 'pallescent'. In some of the latter, e.g. the lectotype of *Achatina marteli pallescens*, lines of arrested growth are highlighted with thin bands of dark brown.

A delicate beaded or slightly semilunar sculpture starts in the second quarter of the first whorl and quickly assumes in the early second whorl the diagnostic sculpture of strikingly coarse, elevated, round or crescentic, discreet but tightly packed beads that are neatly aligned in 5–7 spiral rows. This pattern persists almost uniformly throughout the second whorl. In the mid-third whorl, the transverse rows become greatly compressed, producing growth wrinkles and converting the beads into transverse welts 2–3 times as long as wide. This doubtless marks the first postemergent growth. Adapertural to this, the growth wrinkles become prosocline, the sculpture gradually becomes less compressed, the spiral striae become more numerous and deeper, and the individual welts become larger, more variable in size, more rectangular, and often cleft. The remarkably evenly and closely spaced coarse growth wrinkles embrace and intensify the prosocline rows of welts, producing the characteristic prominent ribbed sculpture of this species. Apically, the ribs may bifurcate and form crenulations. Below the periphery, the welts rather abruptly reduce to one-quarter their calibre, or are absent, leaving prominently the growth wrinkles. An extremely fine decussate micromesh of the periostracum appears on the last whorl of some specimens. It is more noticeable on the shiny inner layer of the periostracum where the latter is exposed through wear or injury. It is apparent that the micromesh is formed at the time that the inner periostracal layer is laid down and that it is largely obscured by the preformed, smoother outer periostracal layer. It is likely that the micromesh assists structurally in bonding the two periostracal layers.

SOFT ANATOMY. No known alcohol preserved specimens.

TYPE MATERIAL. In his description of this species and its synonymous unicolorous 'variety *pallescens*', Dautzenberg (1901) announced that he was dedicating them to Colonel Martel and that specimens had been collected by R.P. Guillemé 'en nombreux exemplaires' in the region of Lake Tanganyika. He did not specifically designate types and paratypes, although he selected a fine flamed specimen and an equally fine unicolorous specimen that were photographed, both in apertural view only, as representative of the

two proposed taxa. These are in the type collection in Bruxelles (IRSN) and are here selected as lectotypes of Dautzenberg's *Achatina marteli* and *A.m. pallescens*, respectively (Figs. 37–40; Table 7). As he pointed out in a footnote in the original descriptions, the pronounced flame pattern of his figure 1 unfortunately did not reproduce well. Pilsbry's copies (1905) therefore reflected this deficiency. In this species, neither the lack of colour pattern nor the greater degree of ventricosity is taxonomically valid for establishing a trinomen.

In the IRSN collection there are several mixed lots totalling 48 mostly juvenile, damaged or weathered specimens. All these specimens were very carefully examined in the present study and were found to be a mixture of the flamed and unicolorous forms of this species and, in addition, juveniles of *Bequaertina pellucida* and *Achatina craveni*. These cannot reasonably be considered to have been a part of Dautzenberg's type series. Dautzenberg, however, did distribute his specimens widely. Those bearing the type locality and R.P. Guillemé as the collector are here selected as paralectotypes. The known distribution of these flamed/unicolorous specimens are BMNH 1/0, NMW 1/1, IRSN 8/5, MCZ 2/1, MRAC 7/1, NMB 2/1, MNHN 6/1, NHMW 1/0.

Table 7 *B. marteli* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl	% LW/L	% W/L	
6½	68.3	34.0	42.3	20.8	55.4	81	50	Mpala (IRSN) PLec
6¼	67.2	38.6	39.1	22.2	54.4	81	57	Mpala (IRSN) Lect
6	63.7	33.2	37.7	19.6	51.5	81	52	<i>A.m.p.*</i> Mpala (IRSN) Lect
6¼	62.9	32.3	36.7	18.2	49.8	79	51	<i>A.m.*</i> Mpala (MCZ) 97929 PLec
6	60.8	34.8	38.0	19.4	51.3	84	57	Mpala (MNHN) PLec
5¾	58.4	32.3	37.3	18.5	49.0	84	55	Mpala (MRAC) 5129 PLec
654.032.233.817.043.78160	54.0	32.2	33.8	17.0	43.7	81	60	Mpala (MNHN) PLec
5¾	48.4	26.9	32.1	15.0	39.8	82	55	Mpala (BMNH) PLec 1937.12.30.1934
5½	48.4	27.9	32.0	16.7	40.5	84	58	Mpala (MRAC) 5125 PLec
6	48.4	27.3	31.0	15.5	39.6	82	56	Mpala (MRAC) 5131 PLec

Total specimens examined: 69. Sources: BMNH, IRSN, MCZ, MNHN, MRAC, NHMW, NMB, NMW.

TYPE LOCALITY. Mpala (= Pala) 6° 45' S, 29° 31' E, region of Lake Tanganyika, Zaire (cf van Burggen, 1988:9).

DISTRIBUTION. All specimens examined are from the type locality. Verdcourt kindly sent the author a photograph of a specimen, which earlier had been identified as *Achatina tavaresiana* (Pain & Verdcourt, 1962; Verdcourt, 1966). This specimen is clearly *B. marteli* and establishes this species in Tanzania on the eastern shore of Lake Tanganyika in the Mahari Peninsula at Nkungwe (= Kungwe) 6° 07' S, 29° 48' E. It was collected in 'litter in thick scrub at head of stream, altitude 4500 ft'. With the many locality records known for *B. pellucida*, including Mpala, it is strange that the distribution of the present species is, to date, so contrastingly limited.

REMARKS. This is the least fragile and the most boldly sculptured species in the genus. Phylogenetically, it appears to stand between *B. pellucida* and *B. pinto*. Mixed lots of *B. marteli*, *B. pellucida*, and *Achatina craveni* suggest that these species are sympatric. The juveniles in particular are confusable. By far the largest series of this species is to be found in Bruxelles (IRSN).

Bequaertina pinto (Bourguignat, 1889)
Figs. 41–51

Serpaea pinto

Bourguignat, 1889:86, pl. 4, fig. 4.

Achatina fragilis

Smith, 1899:591, pl. 35, figs. 3, 4 (*non Achatina fragilis* Deshayes, 1864); Ancey, 1902:278, text fig. 6; Pilsbry, 1904:63, pl. 9, figs. 25, 26 (ex Smith); Dautzenberg & Germain, 1914:26.

'*Achatina* . . . sp. nov?'

Ancey, 1902:277, text fig. 4.

Achatina pinto

Pilsbry, 1904:63, pl. 41, fig. 8 (ex Bourguignat); Bequaert, 1950:11; Verdcourt, 1966:111, 1983:219.

Achatina nyikaensis

Pilsbry, 1909:113, 1919:79; Connolly, 1925:168, 1939:321; Germain, 1935:9; van Bruggen, 1965:81, 1988:10; van Bruggen & Meredith, 1984:161.

Callistoplepa nyikaensis

Bequaert & Clench, 1934c:115, 116.

Callistoplepa thielei

Bequaert & Clench, 1934c:115, pl. 2, figs. 8–10, 12.

Callistoplepa nyikaensis

Verdcourt, 1966:111, 1983:219; Meredith, 1983a:29, fig. 10, 1983b:247.

SHELL. Shell thin, fragile, highly variable in shape, usually elongate-ovate or ovate-subsuccineiform, but may be ovate, globose-ovate or slender conic-ovate. Whorls 6–6½, rarely slightly larger. Apex obtuse; vaguely mammillate in some specimens. Spire usually inscribes a short broad based triangle that appears to be nearly equilateral, 27–36% of shell length. Less commonly, the spire is more produced, with the sides of the connate triangle appearing longer than the width of the base, 37–43% of shell length; such specimens may or may not have a more slender last whorl. Sutures fine, distinct, deeply impressed, quite regular, but may be faintly crenulate in the last part of the sixth whorl. Whorls slightly, moderately, or distinctly convex, usually expanding rapidly to form a large last whorl, 84% of shell length; range for 3½–6¾ whorls, 78–87% (n = 87). Aperture ovate-acuminate; charac-

teristically widest slightly below middle; translucent pale milky opalescent within; fine, closely aligned internal riblets mirror the external sculpture. Columella concolorous or white; long, slender, feebly arcuate or nearly straight; truncated obliquely or abruptly. Outer lip extremely thin, fragile, somewhat receding, arcuately skewed and evenly rounded toward the base. Parietal callus not apparent in young or fresh specimens; thinly calcareous white in others.

Nearly 90% of the specimens examined in the present study (77/87) were essentially unicolorous in a colour gradient from pale olivaceous yellow to olivaceous brown to deep olivaceous green. In individual specimens, the colour tends to be quite uniform, except for darker bands where there was cessation of growth. Because of their very thin two periostracal layers, the apical whorls, which are pale straw colour, soon become calcareous white with wear and exposure. Ten of the specimens examined had on their lower whorls, very faint, narrow light castaneous irregular, sometimes interrupted, transverse stripes that were one-half to one-third the width of the ground colour between them. In some specimens, only a fraction of a whorl was involved.

Extremely fine spiral engraved lines appear at the end of the first whorl. Transverse lines appear in the second whorl, giving rise to depressed beads that become more conspicuous and more abundant until near the middle of the third whorl. At that point, which marks the end of the nepionic whorls, the beads become compressed into very narrow transverse ridges. In the fourth whorl, this compression is relieved and a fairly even granulose-cancellate sculpture emerges. In the fifth and sixth whorls, the granulae swell to become welts that occasionally anastomose along the transverse growth wrinkles, with the shallow spiral lines remaining strongly in evidence (cf Bequaert & Clench 1934c, fig. 12). Usually, this sculpture diminishes rapidly in caliber at the periphery, with essentially only the growth wrinkles continuing into the otherwise smooth surface. In other specimens, the sculpture may continue strongly below the periphery, but at a reduced calibre. In still others, subdued patches of this sculpture appear irregularly below the periphery, and perhaps contrastingly so with resumed growth after diapause. Particularly in the parietal area, the dull, tenaceous microscopically granular outer periostracal layer may wear off, exposing the smooth, shiny inner periostracal layer. Only rarely has a periostracal decussate micromesh been observed in this species, and then only spottedly below the periphery in the inner periostracal layer of the sixth whorl, e.g. in the holotype of *Callistoplepa thielei* Bequaert & Clench, 1934c.

SOFT ANATOMY. Alcohol preserved specimens available 29/dissected 17. Tanzania: BMNH 1/1, NHMW (no.47996) 1/1. Malawi: CMNH 13/2, HM 5/5 (all now at RMNH), NG 4/3 (2 now at BMNH), RMNH 3/3. Zimbabwe: NM 2/2. Additional Malawi specimens are in collections HM and NG. No others are known. Most specimens examined were well extended from their shells.

In the individual specimen, the body colour varies from unicolorous pale buff to dark grey. A black thin-lined, coarsely reticulate pattern is characteristically present laterally on the foot. Sole of foot is uniformly pale dusky, without variation in texture. Usually a delineated or diffuse narrow dark grey or black stripe, originating behind each ommatophore, passes posteriorly toward the mantle on either side of the paler neck region. The mantle varies from unicolorous dark or light grey to a grossly maculate pattern. The Chirinda

Forest, Mount Selinda, Zimbabwe field notes of A.C. van Bruggen *in litt.*) record the body colour varying from black to pale grey marbled with black, and the longitudinal stripes varying from white to greyish white.

The short, slender penis (P) and the slightly shorter penis sheath (PS) seem diminutive compared to the relatively gross structures of the basal female conduit. Of the 17 specimens dissected, 11 had the apical-most P and the basal-most basal vas deferens (BVD) projecting slightly above the rim of the PS. In the other 6 specimens, the P was completely covered by the PS, 2 of which were gravid, 2 were over-drowned with consequent eversion of the genital atrium (GA), one was immature and one was severely distorted because of improper fixation. There was no positive correlation in this latter group of 6 with such other possible influencing factors as latitude, shell size, length of penial retractor, month of collection or size of albumen gland. The specimen (NM) depicted in Fig. 17 collected by A.C. & W.H. van Bruggen in Zimbabwe (Vumba Circular Drive, Zonwi River Bridge) has thus been selected as representative of the first group and typical of this species.

In all specimens, the penial retractor (PR) inserts either on the anterior diaphragm, on the body wall of the neck, or at the forward junction of the diaphragm, mantle and body wall. In well extended specimens, it can appear inordinately long. Cutting and spreading the thin-walled PS reveals the slender P and BVD within (Fig. 18). Fine muscle strands pass basally from the PR to cover thinly the apical P. About half way down the P, these strands attach to the smooth, shiny inner surface of the PS and then proliferate into voluminous strands that completely cover the BVD and infuse with the tissues of the basal P and PS. At this level the tissue layers are not distinct, but below the PS the male conduit continues as a short penial atrium (PA) that joins the vaginal atrium (VA). These fuse to form the genital atrium (GA). Strap-like overlapping, glistening eversion muscle bands (EM) connect the basal male and female conduits to the inner right body wall. During precopulatory behaviour, contraction of these muscles cause the GA, then the PA and VA to evert, to protrude as a stimulatory organ, and subsequently to initiate the extroversion of the intromittent organ. In some older specimens, these bands can be so voluminous and so high on the PS that they seriously obscure relationships. The thin-walled BVD passes through the PS to emerge as a much larger, thick-walled apical vas deferens (AVD), which basally functions as an ejaculatory duct and as a support for the thin-walled everted P. About midway apically, the AVD gradually becomes thin-walled until at the AVD/FO junction, it forms a glandular funnel-shaped chamber that internally is crowded with extremely thin epithelial partitions. This may function as a secondary seminal vesicle (SSV). There is no pilaster or verge in this species.

In the basal female conduit, the vagina (V), free oviduct (FO) and the spermathecal duct (SD) form, without distinct delineations, an impressive muscular Y-shaped structure (Fig. 18). Upon dissection, the broad lumen and the prominent longitudinal plicae of the V are seen to be uninterruptedly confluent with those of the SD. In contrast, the lumen of the basal, muscular thick-walled FO is slender and it is confluent with that of the V through a small recessed pore. This arrangement ensures the passage of the intromittent organ into the SD during copulation. The thick-walled FO functions basally as an ovijector; apically its thin walls accommodate the descending eggs. The clavate-elongate

spermatheca (S) (Fig. 17) frequently is apically attenuated because thin fibers firmly attach it 4–5 mm below the AVD/FO junction. That junction, in turn, is held tightly together on the right internal body wall by fibres from the transverse myoseptum. Any contraction or extension thus provides maximum pull in this part of the body. As a result, under certain conditions, the S apex and SD may become inordinately elongate or nearly disappear into a huge sacculate S. Severe contraction of the viscera may even produce the artifact of a tandem bilobed S. The only important character of the S is its consistent position below the AVD/FO junction. The FO, though shorter than the AVD, is conspicuously long, nearly uniformly wide, and approximately twice as wide as the AVD. Although there are thin fascia binding together V, SD, S, FO and AVD, there is no formation of a vaginal rententor per se.

Two specimens were gravid. One from Chinyama, Malawi (HM) was collected in February 1983 (mid-rainy season) and had 56 light yellow, moderately large eggs averaging 6.3×5.2 mm. The other, from Lake Rukwa, Tanzania (BMNH), was collected in 1938 (month not indicated) and had 51 similar eggs measuring 7×5.5 – 6.5 mm. The eggs, without discernible embryos, were closely embraced by uterine tissue folds as depicted by Mead (1950, fig. 48) for *Achatina fulica* Bowdich, 1822.

All specimens dissected showed a remarkably gross development of a trimerous hermaphroditic duct system (Fig. 19). Basally, there is a 10 mm characteristically deeply convoluted portion just distal to the talon. Next, there is a 3×2 mm discreet, compacted saccular portion that appears to be glandular. And finally, there is a 6 mm slender, weakly convoluted portion that quickly forms a series of five larger, tightly convoluted ductules leading to the five gonadal acini buried in the right lobe of the digestive gland. The talon is elongate, capitate and diminutive (1.5×0.5 mm). The spermooviduct is characteristic of the family.

The following anatomical characters distinguish this species from *B. graueri*: basal genital fascia diaphanous; AVD about twice the width of BVD and half the width of FO; P slender, much longer than wide, normally projecting slightly above PS; BVD slender, much longer than wide.

TYPE MATERIAL. For over a century, Bourguignat's (1889) *Serpaea pinto* has been an enigma to conchologists. The principal contributing factor has been the artist's rendering an excessively bold, wide, broadly truncated columella. A second factor is that the exceedingly thin, fragile shell of the only known specimen unfortunately had become broken sometime since it was drawn. The several pieces, including a figure '4' label, had been placed in a separate vial. This specimen (Figs. 41, 42; Table 8) is in Paris (MNHN) and is here considered to be the holotype by monotypy (Code Art. 73(a)(ii); 74(b). Its conchological features and the type locality in eastern Tanzania support the conviction that this is conspecific with Smith's junior subjective synonym *Achatina fragilis* (1899). Pilsbry (1904:1, 21, 63) placed *Serpaea* in the synonymy of *Achatina*, indicated (1909:113) that Smith's name was a primary homonym of Deshayes' fossil species (1864), proposed the replacement name *Achatina nyikaensis*, reproduced Smith's figures [fig. 26 is way too intensely coloured], and perspicaciously placed Bourguignat's species and Smith's species seriatim under *Achatina* in his Manual.

Smith's syntype lot of seven specimens from Nyika Plateau, Malawi, unfortunately contains a single specimen of *Achatina*

Table 8 *B. pinto* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl % LW/L	% W/L	
6½	74.6	42.8	47.6	26.1	62.5	84	57 Nyika Plateau (BMNH) Lect <i>A. fragilis</i> *
6¼	74.4	42.0	46.3	24.6	61.4	82	56 Macequesse (SAM)
6	66.8	40.6	46.9	24.0	58.0	87	61 Nyambadwe (NG)†
6¼	62.2	32.7	38.3	19.5	50.6	81	52 Utengule (ZMB) Holo <i>C. thielei</i> *
6	56.2	37.8	38.0	21.3	47.9	85	67 Bulawayo (RMS)
6	56.0	33.0	35.5	19.6	46.5	83	59 Utengule (BMNH)* Mac Andrew (1563)
6	53.3	27.2	33.0	16.7	43.5	82	51 Chirinda (BMNH)* 1907.7. 25.3
6	50.1	32.6	33.0	19.8	42.4	85	65 Mamboya (BMNH)* 1885.5. 25.47
6	49.7	33.6	31.8	19.5	43.2	87	68 Ngengre (MNHN) Holo <i>S. pinto</i> *
6¼	49.3	27.2	28.3	15.0	38.5	78	55 Tanzania (NHMW)*
5¾	49.3	33.7	34.9	19.3	42.7	87	68 Pemba (SAM)
5¾	43.7	29.0	29.0	17.8	37.2	85	66 Usagara (BMNH)

Total specimens examined: 92. Sources: BMNH, FMNH, HM, IRSN, LNK, MCZ, MNHN, MRAC, NG, NHMW, NM, NMW, RMNH, SAM, SMF, UMMZ, ZMB.

craveni Smith, 1881. Since Smith, as its author, was thoroughly familiar with this latter species, since he did not designate the number of syntypes, and since he separately discussed (p. 35) and figured (figs. 1–4) specimens of both this species (BMNH no.97.12.31.1–7) and *A. fragilis* (BMNH no.97.12.31.8–14) in his 1899 paper, it is here safely assumed that the division between the two adjacent accessioned specimen lots was an inadvertent curatorial error, with no nomenclatural implications for the misplaced specimen. The unicolorous, largest and finest specimen (BMNH no.97.12.31.9) of the six syntypes (Smith's fig. 3, Pilsbry's fig. 25), here shown in Figs. 43, 44 bears a handwritten note, 'Lectotype "3" A.C. van Bruggen, May 1974'. This selection is here endorsed. Other known and examined paralectotypes are single specimens in Berlin (ZMB no.101934) and Vienna (NHMW/R).

Ancey (1902) described and illustrated a specimen which he labelled '*Achatina* . . . *sp. nov.*' from Ugogo (5° 4' S, 34° 4' E). Ancey's collection was distributed widely by Geret and this specimen so far has not been located. However, the very

large aperture, the slender arcuate columella, the transverse stripes, the translucence of the shell showing the pattern through the aperture, and the locality indicate that his specimen is Bourguignat's species.

Bequaert & Clench (1934c) found nine purchased (Hermann Rolle) specimens from Utengule, Tanzania in the Berlin Museum (ZMB) that were marked as new and given a preempted manuscript name, but were undescribed. Although they felt the new taxon 'might perhaps prove to be a local race' of *Callistoplepa nyikaensis*, its more slender, more tapered shape convinced them it should be established as the new species *Callistoplepa thielei*. The largest specimen previously had been broken, so they selected the second largest specimen as the holotype (Figs. 45, 46). In addition to the holotype, they figured two paratypes. This series of four types (ZMB no. 53177) are in Berlin (Kiliyas, 1992). Examination of these types in Berlin in 1989, showed evidence that the paratypes had been broken apparently on their return to Berlin because their fragile shells had been stuffed excessively with cotton, leaving only the holotype undamaged. The five other original specimens, 3 full grown and 2 juveniles, are labeled paratypes (MCZ no. 98686) in the Harvard collection. Three other broken specimens with the same data are in Frankfurt (SMF); there is no evidence that these were seen by Bequaert & Clench.

TYPE LOCALITY. Bourguignat (1889) states, '... provient des environs de l'Ougeregere, vallée du Kyngani, dans l'Oukani'. Inside the lip of the holotype, in Bourguignat's handwriting, is '*Serpaea pinto* Ougeregere (Oukami). A small label bears the inscription 'M. Requin 1846 30'. According to B. Verdcourt (*in litt.*), Ukami is a large geographic district that surrounds and includes the Uluguru Mountains in Tanzania. The Kingoni river and the Ngerengere settlement and stream, however, place the type locality close to 7° 03' S, 38° 31' E, 125 km west of Dar-es-Salaam (cf Verdcourt, 1966:111).

DISTRIBUTION. This is by far the most widespread species in the genus. The 32 recorded localities define a 1800 × 1200 km territory 4–20° S, 27–39° E that includes eastern Zaire, eastern and western central Tanzania, nearly all of Malawi, south central Zambia, southern and eastern Zimbabwe, and far west central Mozambique (Fig. 16). The northern outpost of this species was established in Zaire by R. Grauer in 1910, when he found and preserved in alcohol a specimen in 'the primary forest behind bordering hills of the northwest shores of Lake Tanganyika, 1800–2200 m' (*trans.*) 4° 30' S, 29° 00' E. It is noteworthy that along the west, there is an almost straight N–S line of demarcation 27–28° E from eastern central Zaire to south central Zambia and southwestern Zimbabwe. Connolly, in his writings (1925, 1939) and on some of his specimen labels, juxtaposes the geographic names Macequece (a district in eastern central Mozambique) and Lourenço Marques (the major port now known as Maputo in southern Mozambique). Specimens may have been shipped from this port, but there is no convincing evidence that this species has ever been collected in Mozambique south of the Macequece district. The remarks of Germain (1935:4) seem to clarify when he explains that Portuguese East Africa is generally divided into two large regions separated by the Zambeze River, 'le Mozambique au Nord, le Lourenço Marques au Sud'. When adequate population studies can be

made in this widespread species, valid subspecies may emerge.

REMARKS. This apomorphic species is most closely related to *B. marteli*. Both *Achatina craveni* E.A. Smith, 1881 and *B. pinto* are highly variable and are often confused in collections, particularly where the field data are the same or the individuals are small. Despite rather considerable overlap in the extremes of the conchological characters of these two species, the shell of *A. craveni* can be differentiated on the basis of the following: nepionic whorls smooth; last whorl equals only 70–75% of shell length (vs 80–90%); one to two more whorls for the same length; apex more acute; columella much shorter, broader, straighter and more squarely truncated; finer and deeper granulate-cancellate sculpture; shell usually much less fragile.

The wide distribution and the independently great variability in shell characters, even within a single population, are responsible for the long and confused synonymy of this species. The soft anatomies of antipodal specimens, and many between, support the conclusion that only one species is involved.

Ecological notations with specimen data (HM, NG) indicate that active specimens were found in Malawi lowland evergreen forests, along the banks of earth roads, crawling on leaf litter, and on the underside of banana leaves in the rain. Specimens from Mbeya, Tanzania were found in luxuriant herbaceous vegetation (LNK). The director of the Imperial Institute of Entomology earlier reported that in the Nkoto-Kota district of Malawi there was a 'very serious outbreak in November 1937', implying that this species has the potential under certain conditions of becoming an agricultural pest. In Zambia this snail is known as 'chuzuya'.

The fine series of specimens in BMNH convincingly demonstrates the wide range of variability in the shells of this species (Figs. 41–51).

Bequaertina fraterculus (Dupuis & Putzeys, 1900) Figs. 52, 53

Ganomidos fraterculus

Dupuis & Putzeys, 1900:xiii, text fig. 18.

Callistoplepa fraterculus

Pilsbry, 1905:129, pl. 47, fig. 23 (ex Dupuis & Putzeys); Germain, 1909:90; Pilsbry, 1919:80; Bequaert & Clench, 1934c:114.

SHELL. Shell ovate-turrite, extremely thin, translucent. Whorls 6–6¼. The second and third whorls are comparatively large, long and nearly straight-sided, producing characteristically a collared blunt mammillate apex. The fourth and subsequent whorls are convex and expanded proportionately. Sutures moderately deep. Last whorl large, but not inordinately so, 78% of shell length; range for 6–6¼ whorls, 77–80% (n = 10). Aperture oval, pale milky within. Columella brown, long, slender, nearly straight, obliquely truncated. Outer lip thin, evenly arcuate; receding at base in profile. Parietal callus diaphanous.

Highly irregular castaneous streak and spot brush marks, some of which are closely highlighted with buff adaperturally, are characteristically found on the last whorl; however, these may be reduced to a few obscure dull buff spots more or less limited to the peripheral carina. The earliest signs of this diagnostic colour pattern are seen in the third whorl. The ground colour intergrades from pale horn colour of the

unicolourous nepionic whorls to an obscuring dark olive brown of the last whorl.

Faint, closely oppressed minute crescentic granulations may appear in the second half of the otherwise smooth first whorl. These granulations dominate the second whorl, giving it an evenly, delicately engraved appearance. In contrast, rather bold, diagonally oriented arcuate plicae, arising from the suture below, disrupt this sculpture in a narrow basal zone. This plication, which may start even in the last part of the first whorl, rather abruptly disappears in the third whorl, leaving a delicate, closely aligned series of nearly transverse lirae, uninterrupted except for small, sparse, ghost-like patches of granulations in some specimens. This marks the end of the nepionic whorls. In the fourth and fifth whorls, the lirae become increasingly strongly prosocline, more regular, apically arcuate immediately below the suture, and eventually so prominent that they obscure the growth lines. In the sixth whorl, the lirae become finer, less regular, more nearly orthocline, and often interspersed with short parallel lirellae. In the fifth whorl, spiral lirae, which seem to join rather than interrupt the prosocline lirae, appear somewhat irregularly, producing a slight checkerboard effect, reminiscent of the sculpture of *Achatina tracheia* Connolly, 1929. These spiral lirae, which are quite close together near the suture, irregularly diminish in number and intensity toward the columella. Very shallow malleations, starting subtly in the fourth whorl, intensify the checkerboard effect. A subdued but apparent carina appears at the periphery, where the lirae are seen to bend slightly. The carina is more conspicuous in the younger specimens. Abrasion of the shell along the periphery and along some of the more prominent lirae visually intensifies the carina and the sculpture by exposing the brilliantly shiny inner periostracal layer. The outer layer of the periostracum imparts a characteristically dull, corneous luster to the shell.

SOFT ANATOMY. No known alcohol preserved specimens.

TYPE MATERIAL. Nine of the ten known specimens of this rare species were collected by Dupuis and are considered syntypes. Six of these were identified and labelled as 'cotypes': three in Tervuren (MRAC no.5140–5142) and three unnumbered specimens in Bruxelles (IRSN, General Collection). The seventh specimen (MRAC no.5139) was labelled as the one figured by Dupuis & Putzeys (1900); their figure 18 (reproduced by Pilsbry, 1905) is so generalized that it cannot specifically identify with any of the syntypes. Unfortunately, the apex of this specimen had been broken and cemented together, with a resultant alteration of the shell configuration and length. The damage possibly occurred during the precarious period when the artist had the specimen. Two additional syntype specimens (IRSN) were given to Dauzenberg by Dupuis, one of which was collected in Nsendwe. Under these circumstances, and since the authors did not designate a holotype, the largest and finest of the four MRAC syntypes (no.5140) is here selected as the lectotype of Dupuis & Putzeys' *Ganomidos fraterculus* (Figs. 52, 53; Table 9). The tenth known specimen, acquired by Preston, was passed on to V.W. MacAndrew, and is now in the BMNH. Its apex was damaged and repaired naturally. This, too, most probably was collected by Dupuis and should be considered a paralectotype.

TYPE LOCALITY. The Island of Mvula on the Lualaba River, Zaire. J.C. Bequaert was unable to find this locality on any map (Pilsbry, 1919:11, 19), nor is it listed in the

Table 9 *B. fraterculus* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl % LW/L	% W/L	
6	51.0	28.7	30.0	16.4	40.7	80	56 Mvula (BMNH) PLec
6	50.5	29.0	30.0	16.9	39.3	78	57 Mvula (IRSN) PLec
6¼	50.4	28.5	30.5	17.0	38.9	77	56 Mvula (MRAC) 5140 Lect*
6	47.5	27.4	27.8	16.0	37.5	79	58 Mvula (MRAC) 5139
6	46.3	26.8	28.7	15.5	36.7	79	58 Mvula (MRAC) 5141 PLec
6	44.4	26.6	27.2	14.8	35.0	79	60 Nsendwe (IRSN) PLec
6	44.3	26.4	26.7	14.5	34.0	77	59 Mvula (IRSN) PLec
5¾	40.2	26.4	26.2	14.2	32.6	81	66 Mvula (MRAC) 5142 PLec
5¾	37.5	23.0	22.6	13.2	29.7	79	61 Mvula (IRSN) PLec
5¾	36.5	21.7	22.0	12.2	28.2	77	59 Mvula (IRSN) PLec

Total specimens examined: 10. Sources: BMNH, IRSN, MRAC.

current USBGN series. The only lead is the fact that a single specimen of this species in the Dautzenberg collection (IRSN) bears the data: 'Nsendwe, Congo. P. Dupuis Coll., leg & ded'. At the same time that Dupuis & Putzeys described *Ganomidos fraterculus* (1900), they described the new species *Perideriopsis mvulaensis*, giving its locality as 'île de Mvula (en face de Nsendwe)'. Bequaert in Pilsbry lists Nsendwe as 3° 05' S, 26° E. This location nearly coincides with the important crossroad Kindu-Port-Empain 2° 57' S, 25° 56' E, hence Mvula must be very close to 3° S, 26° E.

DISTRIBUTION. The two known localities for this species are the Island of Mvula and the nearby onshore village of Nsendwe in Zaire. Given the nature of the riverine environment, this species may well be found on other of the many small islands and possibly in shore sites along this northward flowing remote section of the Lualaba.

REMARKS. Phylogenetically, this species appears to stand between *B. graueri* and the plesiomorphic *B. pellucida*. Based on a single specimen from Nsendwe (BMNH, Preston 'L/K 13/11/01'), *B. pellucida* may be sympatric with *B. fraterculus*.

Bequaertina graueri (Thiele, 1911)
Figs. 54–57

Achatina graueri

Thiele, 1911:205, pl. 5, fig. 43; Pilsbry, 1919:78.

Achatina (Cochlitoma) graueri

Pilsbry & Cockerell, 1933:366, pl. 1, fig., 1, 1a.

Callistoplepa graueri

Bequaert & Clench, 1934c:115.

Callistoplepa graueri

Schouteden, 1935a:110; 1935b:287; Oliver, 1983:9.

Callistoplepa babaulti

Germain, 1936:151, text fig. 46.

SHELL. Shell lacrimoid-subsuccineiform; the thick, durable periostracum appears to provide more support than the thin calcareous shell. Whorls 6–6½, rarely 7. Spire tapered, mammillate, elevated-conic, clearly shorter than aperture length. The first 1½ whorls form a bluntly obtuse dome. The second and third whorls expand only slightly, but descend rapidly; this produces the strongly mammillate apex. The fourth and following whorls descend proportionately, are increasingly more convex, but expand rapidly to produce an inordinately large last whorl. Sutures moderately deep, increasingly so between fifth and sixth whorls. Last whorl 80% of shell length; range for 5–7 whorls, 77–83% ($n = 50$). Aperture oval to elongate; very thin blue-white shelly layer within. Columella markedly slender, almost entirely concolourous, slightly arcuate or nearly straight; typically very narrowly and obliquely truncate. Outer lip thin, usually somewhat obscured by the more rapidly advancing thick periostracum, which tends to curl into the aperture in dried specimens. The arc of the outer lip is often greatest below midway and basally extended well below the columellar truncation in the more mature specimens. Parietal callus appears to be virtually absent in the smaller specimens and barely visible in the larger and older specimens.

The first three whorls are unicolorous beige-buff to buff-horn colour. Faint, diffuse wide transverse castaneous bands may emerge in the second whorl and become darker, more conspicuous and fragmented in the third and fourth whorls. These gradually give way to narrow transverse bands of various shades of brown, irregularly appearing coincident or alternating with growth bands. The darkest, broadest bands usually indicate interrupted growth. In some specimens the transverse bands may be essentially absent. Ground colour varies within and between specimens in a spectrum of olive-buff, light yellow-brown, olivaceous brown and medium dark brown. The fifth whorl often has a contrastingly paler ground colour; hence, a 5-whorl specimen, with its short last whorl, may appear to be a different species.

Pronounced spiral striae, usually 5–7, starting in mid-first whorl are offset by beaded or semilunar granules that are irregular in size and not aligned in vertical rows. The spiral rows of granules increase to 12–17 or more and the now very small granules become more uniform, more prominent, and gradually more transversely aligned in the second and third whorls. At the end of the third whorl, there is a prominent delineation that marks the end of the nepionic whorls. At this point, the granulate sculpture is rather abruptly taken over by thin, slightly prosocline growth wrinkles that increase in size and number until they dominate in the fourth whorl. In the fifth whorl, there is a reemergence of the granulate sculpture in the form of notched, subquadrate, tile-like plates that often resemble the block letters K, H, W, V, Y & M, as is strikingly seen in *Achatina reticulata* Pfeiffer, 1845. This reappearance of the granulate sculpture, accentuated by the deeper spiral striae, dominates the fifth whorl, although the growth wrinkles continue to increase in calibre and become

subcrenulate apically. In the usually somewhat darker coloured last whorl, the granulate sculpture is once again greatly reduced, but may be highlighted here and there by an isolated sporadic deep section of a spiral stria. The earliest malleations appear subtly in the third or fourth whorl and intensify in the following whorls. They consist of usually short spiral or diagonal ridges that join or distort the growth wrinkles to form a coarse, irregular raised network of welts. Often entering into this is a very faint elevation at the periphery, below which the otherwise nearly uniform sculpture is reduced. An occasional specimen is entirely without malleations. Their irregular appearance is probably explained by thin shell, tough periostracum, and environmental impacts. Continued shell deposition from within 'fixes' the dents in place. Rarely is the outer layer of the thick periostracum broken enough to reveal the shiny inner layer.

SOFT ANATOMY. Alcohol preserved specimens available 82/dissected 9. Zaire: MRAC (Mulungo, no.204.632–633) 2/2; (Kahusi-Tshibati no.610.302–305, 342–343) 79/6; ZMB (lectotype) 1/1. Unfortunately, all dissected specimens except the lectotype, were exposed excessively to formalin during their preservation; thus, even with prolonged special treatment, their tissues remained hard and the specimens were exceedingly difficult to dissect. Pilsbry and Cockerell (1933) described the living animal as very pale ochreous with head and broad based tentacles faintly bluish.

Clearly, the most conspicuous and characteristic aspect of the basal genital conduits is the vaginal retentor (VR) muscle system, grossly dominating in ventral view (Fig. 20). Slender, parallel, glistening, partly fused muscle bands pass ventrally from the vagina (V) to the right body wall along a dorsolateral line from immediately posterior to the genital aperture to the junction of the mantle and the right body wall. From the left side of the vagina, this system gives rise to a series of muscle bands that starts at the penio vaginal angle and binds tightly together the equally prominent apical vas deferens (AVD) and the free oviduct (FO). A more bold series of distinct, but laterally fused muscle bands pass from the left lateral aspect of the AVD to the same right dorsolateral line of attachment, further obscuring the basal genital structures. (These bands are shown cut short in this figure.) Apically this whole muscle system is reduced largely to a thin, transparent membrane attached to the junction of the AVD and the FO. At this same junction, a similar membrane passes to the spermatheca (S) and attaches it to the FO. The S is proportionately extremely large in this species. In four of the nine specimens examined, the slender apex of the S is folded back on itself, as shown here; this is apparently a common artifact of preservation. In the rest, the apex is extended, and although it may appear to go apically beyond the junction of the AVD and FO, it is not attached to the spermoviduct (SO) as it is in many achatinids. The spermathecal duct (SD) is so short and broad that when the S is gorged, it seems to be sessile on the V.

Short, often diagonal or anastomosing muscle bands, separate or combined, are found at the base of the penis sheath (PS) and the V. These eversion muscle bands (EM) initiate the precopulatory extroversion of the genital atrium (GA). The PS normally completely envelops the short, diminutive penis (P); in only one of nine specimens, the apical P projected slightly. The penial retractor (PR) has its origin on the apical P and inserts on the mid-forward diaphragm at or near the junction with the body wall. A single specimen,

shown here, had a bifurcate insertion; a multiple insertion is not rare in the achatinids. At the origin of the PR, the muscle fibrils enshroud smoothly and completely the apical P and the robust basal vas deferens (BVD), greatly obscuring the relationships in the basal male conduit (Fig. 21). Contributing to this, the PS is free from the P only in the approximate upper half of the left side. On the right side, fibrils from the PR extend basally to form a dense webbing that seems to invade the substance of the outer wall of the P and the inner wall of the PS. Below the PS, this infusion of tissues, along with the EM, obscurely defines the wall of the penial atrium. This atrium connects the lumina of the P and GA (Fig. 22). The lumen of the P is thickly carpeted with vermiculate rugae, which become slender and elongate near the GA, resembling the plicae of the basal V. No verge or pilaster is present. Eccentrically in the apex of the P, a small aperture leads to the narrow lumen of the extremely thick-walled BVD and AVD. These two structures provide the physical support for the extroverted, highly expansile P. Since they have supportive and ejaculatory functions, they may explain the extreme development of the VR. Approximately 8–10 mm basal to the junction of the AVD and FO, the lumen of the AVD enlarges considerably and forms an elongate, thin-walled chamber, which conceivably functions as a secondary seminal vesicle (SSV). Apically this chamber becomes saccular with thin elongate rugae.

A single specimen (610.343) was gravid. Six large, fully formed eggs, 9.5×6.5 mm, were in the apical (oviductal), cream coloured portion of the spermoduct; no eggs were in the contrastingly light brown uterine basal portion. This specimen and the five others in the same lot had robust, mature coloured, fully formed reproductive tracts. The field data thus indicate that in the Kivu, breeding takes place in October.

Kidney is large, typical of the subfamily, broad anteriorly and truncated posteriorly. Five ovotestis acini are embedded in the columellar surface of the right (apical) lobe of the digestive gland. The inconspicuous anterior aorta is on the left posterior surface of the lung, where it penetrates the diaphragm. The hermaphroditic duct, similar to that of *B. pinto* (Fig. 19), is trimerous with an abruptly enlarged saccular central portion, 5.3×2.4 mm.

The following anatomical characters distinguish this species from *B. pinto*: basal genital fascia gross, forming a VR with a massive system of muscle bands; AVD, BVD and FO are all about the same width; P is strikingly short and stubby, normally retained entirely or nearly entirely within the PS; BVD wide, about as long as wide.

TYPE MATERIAL. Thiele (1911) described this species from a single mature specimen (ZMB no.101937) in the Schubotz collection and two small juvenile specimens from the Grauer collection. The mature specimen is nearly full grown but only moderately large (Figs. 54, 55; Table 10). Thiele's fine line illustration shows it slightly larger than natural size in apertural view only. This specimen, whose soft parts are in alcohol, I labelled as the lectotype of Thiele's *Achatina graueri* when I examined it in East Berlin (ZMB) in August 1989. At that time, the single available very dark coloured juvenile specimen (Table 10) therefore was labelled paralectotype. Since then a second small paralectotype has been found there and so labelled by Kilius (1992).

Germain (1936), without any apparent knowledge of Thiele's species, described and figured the junior subjective

synonym *Callistoplepa babaulti* from two specimens collected by Babault in Kitembo, Kivu, comparing it only with *C. marteli*. The two Paris syntypes (MNHN) are large, typical specimens of *Bequaertina graueri* (Table 10). The larger, finer specimen is here selected as the lectotype of Germain's *C. babaulti* (Figs. 56, 57).

TYPE LOCALITY. Idjwi Island (= Kwidschwi, Kwidjwi, Idjewi), Lake Kivu, Zaire $2^{\circ} 09' S$, $29^{\circ} 04' E$.

DISTRIBUTION. This species occupies a 450 km long, narrow, north-south corridor in the upper Rift Valley of Zaire between Beni and Uvira (Fig. 16). So far, it has been found only as far west as Kitembo and projects slightly east of Zaire into Lobengera Mission, Rwanda and into Ibanda, Uganda. Eventually, it will also be found in Burundi.

REMARKS. This is the largest and most distinctive species in the genus. It is most closely related to *Bequaertina fraterculus*. Because of its size and colour, and because in some localities it is sympatric with *Achatina stuhlmanni* von Martens, 1892, it has been confused with that species. However, since *A. stuhlmanni* has a shorter, broader spire, a more obtuse apex, and a distinctive spirally fine-combed wavy sculpture (Bequaert & Clench, 1934a:3), it can readily be

Table 10 *B. graueri* - Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl % LW/L	% W/L	
7	93.2	45.7	52.3	26.6	71.8	77	49 Katana (MRAC) 610.304
6¼	89.7	47.0	55.5	28.4	72.6	81	52 Tshibinda (MRAC) 5115
7	89.3	43.6	50.7	25.5	70.0	78	49 Katana (MRAC) 610.302
6¼	78.4	42.5	46.8	24.3	62.5	80	54 Kitembo (MNHN) Lect <i>C. babaulti</i> *
6	77.0	38.6	45.9	23.5	63.0	82	50 Uvira (MRAC) 607.170
6¼	71.8	41.4	41.9	23.4	56.1	78	58 Kitembo (MNHN) PLec <i>C. babaulti</i>
6	62.0	36.5	37.8	20.6	49.1	79	59 Idjwi (ZMB) 101935 Lect <i>A. graueri</i> †*
5¾	49.8	29.1	31.8	16.4	40.0	80	58 Idjwi (MCZ)
6	49.2	22.8	31.0	14.5	39.5	80	46 Beni (MRAC) 5119
5¼	42.0	25.7	27.0	14.0	33.0	78	61 Idjwi (ZMB) 101936 PLec <i>A. graueri</i>

Total specimens examined: 54. Sources: IRSN, MCZ, MNHN, MRAC, NMW, RMNH, SMNH, UMMZ, ZMB.

distinguished. Pilbry & Cockerel (1933) reported seeing two living specimens 'crawling about 5 feet up on the trunk of a tree in the forest above Tshibinda at about 2100 m' in Zaire. The largest collection of this species, including many alcohol specimens, is to be found in Tervuren (MRAC). *B. graueri* is the type species of the genus.

Radulae and jaws

D'Ailly (1896:69) was the first to describe and illustrate the radulae of *Callistoplepa shuttleworthi* and *C. barriana*. Pilbry (1904:ix, xv) referred to d'Ailly's work but reproduced only the illustration of the latter species. He also reported (p. 72) that G. Schacko (1881) (*nec* 'Schako') found 'A. *pulchella* has . . . a very small central tooth'. The present work shows Schacko's specimen was therefore misidentified. Thiele (1929:560) examined and illustrated in part the radula of *C. shuttleworthi*. He also examined but did not illustrate the radula of *Leptocala mollicella* and pointed out that the middle tooth was a little smaller than the neighbouring teeth. Possibly on the basis of this observation, he prophetically juxtaposed '*Callistoplepa*' and *Leptocala*. More recently, Ortiz & Ortiz (1959:47) also illustrate the radula of *C. shuttleworthi*, but the focal plane of the microscope was apparently too low and the configurations of the teeth are misleading. The radulae in the present project were prepared according to the recommendations of Solem (1972) and the emphasis has been placed on the rachidian teeth and the adjacent laterals.

Because the soft anatomies of the four callistoplepine species are so similar, it was not surprising to find the radulae of *C. barriana*, *C. shuttleworthi* and *L. mollicella* (Figs. 58–63) to be remarkably similar. This fact supported the earlier decision to conserve intact the odontophores of the two extant soft anatomy specimens of *L. petitia*. It is assumed with confidence that the radula of this latter species is essentially like the others. In those examined, all have bold rachidian basal plates and a broad functional rachidian tooth that is one-half to two-thirds the size of the adjacent lateral teeth. A second type of tooth is found in the first series of laterals, which similarly consists of broad, solitary mesocones, but with conspicuous laterally asymmetrical basal plates. A third type of tooth arises in the second series of laterals, wherein the mesocones angle increasingly more mesad and small ectocones gradually arise. These merge almost imperceptibly into a fourth type, the tricuspid marginals with minute irregular endocones, broad shorter serrate mesocones, and increasingly reduced basal plates that no longer contact the teeth posterior to them. The greatest irregularity within and between specimens occurs in the gradient between the bicuspid laterals and the tricuspid marginals. Hence the following formulae (tooth numbers from centre to right) are only approximate: *C. barriana* C-31–55–84, *C. shuttleworthi* C-17–28–49, and *L. mollicella* C-19–28–66.

The available radula specimens in only two of the five *Bequaertina* species have produced an incomplete and somewhat confusing picture in this genus. The basal genital systems of *B. pinto* and *B. graueri* are fundamentally similar – both reflecting affinities with the Zaire Basin subgenus *Achatina* (*sensu* Bequaert, 1950). It thus was anticipated that the radulae also would be similar. The radula of *B. pinto* (Figs. 64, 65), not surprisingly, was found to be of the same type as that of *Achatina craveni* E.A. Smith, 1881 (Figs. 68, 69). Both have greatly diminished, essentially nonfunctional

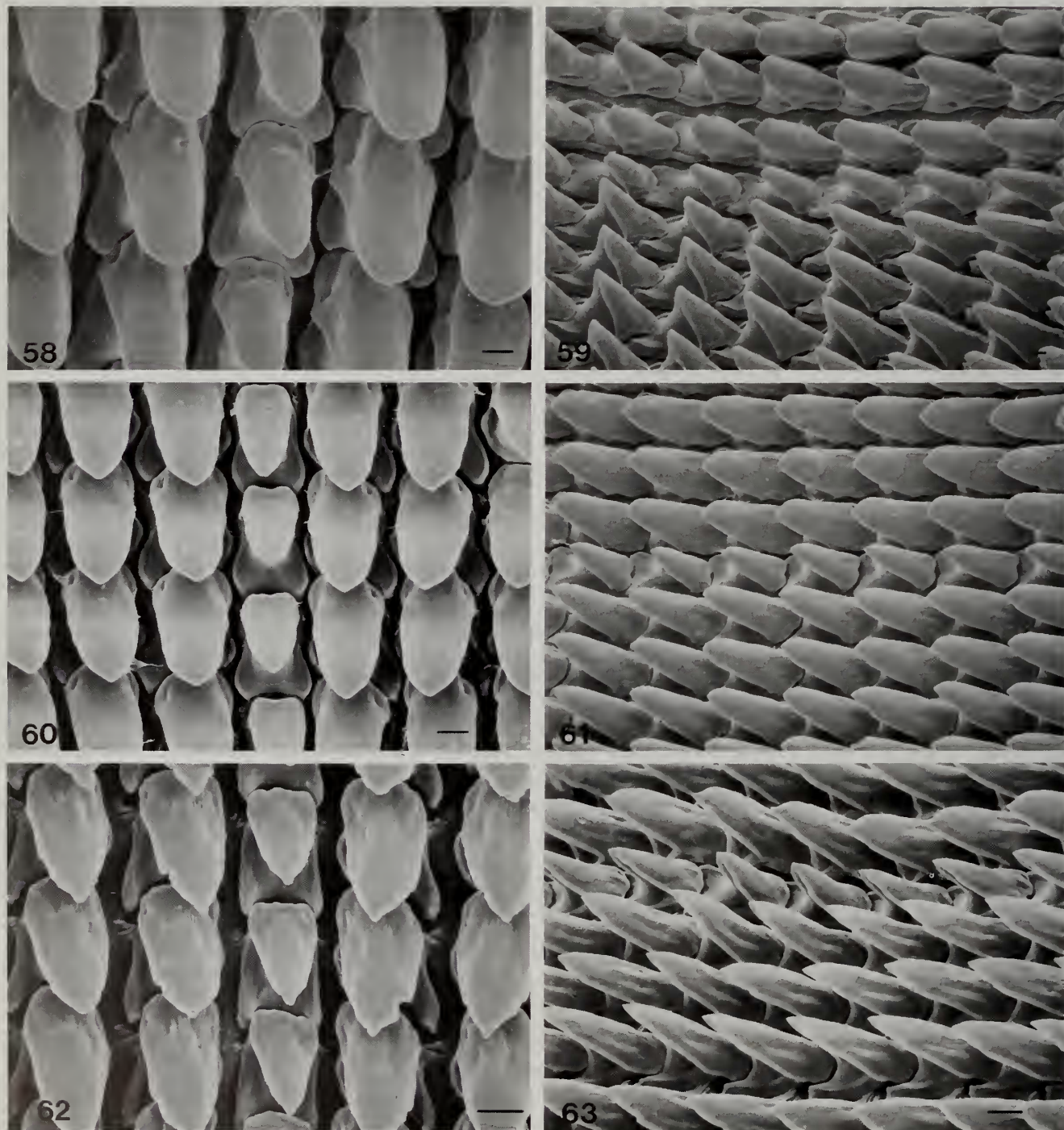
rachidian teeth that are almost concealed by the adjacent laterals. And both have broad based, nearly tricuspid laterals with angular ectocones, broad mesocones and endoconal flanges. In addition, the mesocone column of each lateral tooth directly contacts and supports the broad basal plate of the tooth immediately posterior to it. It should be noted that *A. craveni*, on the basis of its soft anatomy, belongs in Bequaert's subgenus *Achatina* rather than where he has placed it in his subgenus *Lissachatina*. The surprise came in the radula of *B. graueri* (Figs. 66, 67), with its large functional rachidian tooth, attenuated massive basal plates, more restricted contact support between horizontal rows of teeth, and an imperceptible gradient into the marginal teeth. Within the genus, *B. pinto* and *B. graueri* are at the conchological, geographic and ecological antipodes. The known plasticity in molluscan radulae suggests that undetermined different feeding demands in dissimilar habitats have produced the contrasts in the radulae of these otherwise two closely related species. *B. graueri* and *B. fraterculus* appear to be very closely related conchologically. There is a question now whether the radulae will support this assumption. In reality, the relationships in *Bequaertina* will not be understood until both the soft anatomies and radulae of *B. fraterculus*, *B. pellucida* and *B. marteli* are known. Radula formulae: *B. pinto* C-42–25, *B. graueri* C-59, *A. craveni* C-34–24.

The castaneous callistoplepine jaw forms an unusually broad middle section that quickly tapers on each side to about half its width and curves inward at the ends into a collariform structure. Its surface is featureless except for microscopic horizontal growth increments best seen under transmitted light. Measurements: *C. barriana* 2 × 1.3 mm, *C. shuttleworthi* 1.5 × 0.6 mm, *L. mollicella* 1.7 × 0.4 mm. The illustration of Ortiz & Ortiz (1959:46) for *C. shuttleworthi* appears excessively broad.

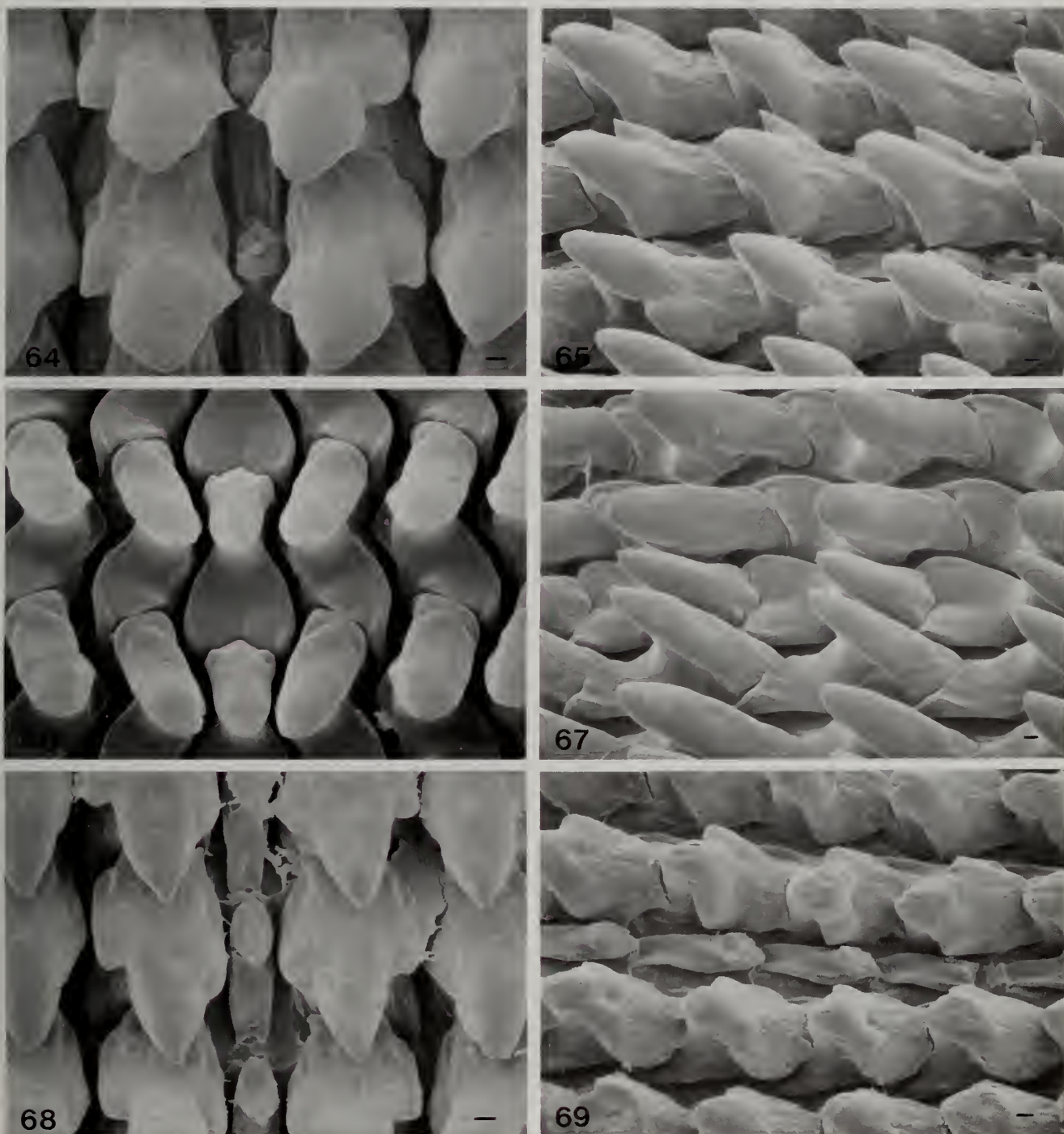
The jaw of *B. pinto* forms a light castaneous nearly uniformly slender rainbow arc, 5.5 × 1.1 mm, with ca 36 irregularly placed vertical ridges. In *B. graueri* the jaw forms a lower arc, 4.4 × 1.3 mm, with very obscure vertical lineations.

The more slender jaw of *A. craveni* forms a fulvous, somewhat depressed arc, 4.5 × 0.7 mm, with ca 35 fairly uniformly distributed vertical riblets.

ACKNOWLEDGEMENTS. Special thanks are given to the curators and their assistants of 28 museums, and to three private collectors, all individually referred to in the **Acronyms – Institutional & Personal Collections**. I am especially grateful to Drs A.C. van Bruggen (Rijksmuseum van Natuurlijke Historie, Leiden), B. Verdcourt (Royal Botanic Gardens, Kew), and W.F. Sirgel (Stellenbosch University) for reviewing the manuscript and offering valuable suggestions; and to Dr P.K. Tubbs, Executive Secretary of the International Commission on Zoological Nomenclature, for consultations on the Code. I am also indebted to many others who have provided important assistance, among them: Donald B. Sayner, Charlotte Erstein and Virginia Childs of the Scientific Illustration staff at the University of Arizona for photographs in Figures 27–42, 45–46, 52–57; the Photography Service staff of the British Museum (Natural History) for photographs in Figures 23–26, 43–44, 47–51; David L. Bentley of the Electron Microscope Facility, Division of Biotechnology, and Professor Michael A. McClure, both of the University of Arizona, for assistance in the SEM photographs; Emilee M. Mead of the University of Arizona Teaching Center who drew the map and prepared the photographic layouts; Yolanda Baldonado Whigham of the U.A. Department of Ecology and Evolutionary Biology for word processing; and my wife Eleanor who has helped in countless ways.



Figs 58–63 Dorsal and dorso-right lateral views of radulae: 58, 59 *Callistoplepa barriana* (SMF, O. Boettger). 60, 61 *C. shuttleworthi* (SMNH no. 10). 62, 63 *Leptocala mollicella* (MRAC no. 795.638).



Figs 64, 65 *Bequaertina pintoï* (BMNH no. 1953.8.15.562–564, mixed lot). 66, 67 *B. graueri* (MRAC no. 204.633). 68, 69 *Achatina craveni* (BMNH no. 1953.8.15.562–564, mixed lot). Bar scale = 1 μ m.

ACRONYMS – INSTITUTIONAL & PERSONAL COLLECTIONS

AMNH	New York: American Museum of Natural History (W.K. Emerson)
ANSP	Philadelphia: Academy of Natural Science (A.E. Bogan)
BMNH	London: British Museum (Natural History) (P. Mordan, F. Naggs)
BV	Kew, Royal Botanic Gardens: Bernard Verdcourt
CMNH	Pittsburg: Carnegie Museum of Natural History (J.E. Rawlins)
FMNH	Chicago: Field Museum of Natural History (A. Solem)
GNM	Göteborg: Naturhistoriska Museet (I. Levinsson, H.W. Waldén)
HM	Newquay, Cornwall, England: Hazel Meredith
IRSN	Bruxelles: Institut Royal des Sciences Naturelles (J. van Goethem)
LNK	Karlsruhe: Landessammlungen für Naturkunde (H.W. Mittmann)
MCZ	Harvard: Museum of Comparative Zoology (K.J. Boss)
MNHN	Paris: Muséum National d'Histoire Naturelle (S. & A. Tillier)
MRAC	Tervuren: Musée Royal de l'Afrique Centrale (P.L.G. Benoit, F.A. Puylaert)
NG	Blantyre, Malawi: W. Noel Gray
NHMB	Bern: Naturhistorisches Museum (J.J. Oberling)
NHMW	Wien: Naturhistorisches Museum Wien (E. Wawra, O.E. Paget)
NM	Pietermaritzburg, South Africa: Natal Museum (R.N. Kilburn)
NMB	Basel: Naturhistorisches Museum (C. Stocker-Unterländer)
NMW	Cardiff: National Museum of Wales (A. Trew, P.G. Oliver)
RMNH	Leiden: Rijksmuseum van Natuurlijke Historie (A.C. van Bruggen, E. Gittenberger)
RMS	Edinburgh: The Royal Museum of Scotland (D. Heppell)
SAM	Cape Town: South African Museum (J. Pether)
SMF	Frankfurt: Forschungsinstitut Senckenberg Natur-Museum (R. Janssen)
SMNH	Stockholm: Naturhistoriska Riksmuseet (A. Warén, C. Holmquist)
UHZI	Hamburg: Universität Zoologisches Institut und Museum (R. von Cosel)
UMMZ	Ann Arbor: University of Michigan Museum of Natural History (J.B. Burch)
USNM	Washington, D.C.: U.S. National Museum of Natural History (R. Hershler)
UUZM	Uppsala: Universitets Zoologiska Museum (Å. Franzén, L. Wallin)
ZMB	Berlin: Museum für Naturkunde der Humboldt-Universität (R. Kilias)
ZMUC	København: Zoologisk Museum – Universitet (J. Knudsen, T. Schiøtte)
ZSM	München: Zoologische Staatssammlung (R. Fechter)

REFERENCES

- Ailly, A. d' 1896. Contributions à la connaissance des mollusques terrestres et d'eau douce de Kaméroun. *Bihang till K. Svenska Vetenskaps-Akademien Handlinger*, 22: 1–137.
- Ancy, C.F. 1888. Catalogue des mollusques terrestres et fluviatiles récoltés sur la côte occidentale d'Afrique par M. le cap. Vignon. *Bulletins de la Société Malacologique de France*, 5: 65–76.
- 1898. Note on the generic names of two groups of Achatinidae. *Nautilus*, 12: 92.
- 1902. Remarques sur différents espèces peu connues du genre Achatina. *Journal de Conchyliologie*, 1902: 273–280.
- Bequaert, J.C. 1950. Studies in the Achatininae, a group of African land snails. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 105(1): 1–216.
- & Clench, W.J. 1934a. Studies on African land and fresh-water mollusks. III. West African Achatinae related to *Achatina balteata* Reeve. *American Museum Novitates*, No. 705, 1–16.
- — 1934b. Studies of African land and fresh-water mollusks. IV. Descriptions of four presumably new Achatinidae; with notes on the genus *Leptocola*. *Revue de Zoologie et de Botanique Africaines*, 24: 269–276.
- — 1934c. Studies of African land and fresh-water mollusks. V. Three new Achatinidae in the collections of the Berlin Zoological Museum. *Revue de Zoologie et de Botanique Africaines*, 26: 112–119.
- Böttger, O. 1905. Beitrag zur Kenntnis der Land-, Süßwasser- und Brackwasser-Mollusken von Kamerun. *Nachrichtsblatt der Deutschen Malakologischen Gesellschaft*, 1905: 153–184.
- Bourguignat, J.R. 1889. Mollusques de l'Afrique Equatoriale de Moguedouchou a Bagamoyo et de Bagamoyo au Tanganika. Méric D. Dumoulin et Cie, Paris.
- Bruggen, A.C. van 1965. Two new species of Achatinidae (Mollusca, Gastropoda Pulmonata) from the Drakensberg Range, with general remarks on South African Achatinidae. *Revue de Zoologie et de Botanique Africaines*, 71: 79–91.
- 1978. Land Molluscs. pp. 887–923. In: Werger, M.J.A. (Ed) *Biogeography and Ecology of Southern Africa* W. Junk, The Hague.
- 1988. A record of the genus *Cerastua* (Mollusca, Gastropoda Pulmonata: Enidae) from Zambia, with a preliminary list of the terrestrial molluscs of that country. *Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen*, Ser. C, 91: 1–17.
- 1989. The Dahomey Gap as evidenced by land molluscs, a preliminary report resulting from a reconnaissance of the literature. *Basteria*, 53: 97–104.
- & Meredith, H.M. 1984. A preliminary analysis of the land molluscs of Mala i. pp. 156–171. In: Solem, A. & van Bruggen, A.C. (Eds) *World-wide Snails; Biogeographical Studies on Non-marine Mollusca* E.J. Brill/Dr. W. Backhuys, Leiden.
- Columbia Lippincott Gazetteer Of The World. 1952. Columbia University Press, New York.
- Connolly, M. 1925. The non-marine mollusca of Portuguese East Africa. *Transactions of the Royal Society of South Africa*, 12: 165–170.
- 1939. A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum*, 33: 1–660.
- Cox, L.R. 1960. General characteristics of Gastropoda. pp. 184–169. In: Moore, R.C. (Ed) *Treatise on Invertebrate Paleontology*. University of Kansas Press & Geological Society of America.
- Cross, H. & Fischer, P. 1869. Nécrologie. *Journal de Conchyliologie*, 17: 108.
- Dautzenberg, P. 1901. Description de trois mollusques nouveaux provenant de l'état indépendant du Congo. *Annales, Société Royale de Malacologie Belgique*, 36: 3–7.
- 1921. Contribution à la faune malacologique du Cameroun. *Revue Zoologique Africaine*, Bruxelles, 9: 87–192.
- & Germain, L. 1914. Récoltes malacologiques du Dr. J. Bequaert dans le Congo Belge. *Revue Zoologique Africaine*, 4: 1–73.
- Deshayes, G.P. 1824–37. Description des coquilles fossiles des environs de Paris. *Animaux sans Vertébrés*, 2: 64–65.
- 1864. Description des animaux sans vertébrés découverts dans le bassin de Paris. *Animaux sans Vertébrés*, 2 (supplément): 839.
- Dupuis, P. 1923. Notes malacologiques concernant la faune de l'Afrique continentale et insulaire. *Annales, Société Royale Zoologique et Malacologique de Belgique*, 53: 80–83.
- & Putzeys, S. 1900. Diagnoses de quelques coquilles nouvelles provenant de l'état indépendant du Congo. *Annales, Société Royale de Malacologie Belgique, Bulletins des Séances*, 35: 13–14.
- Fulton, H.C. 1920. Molluscan notes IV. *Proceedings of the Malacological Society of London*, 14: 3–4.
- Germain, L. 1905. List des mollusques recuilles par M.E. Foa dans le lac

- Tanganyika et ses environs. *Bulletin, Muséum National d'Histoire Naturelle, Paris*, 1905: 254–261.
- 1908. *Mollusques du Lac Tanganyika et des ses environs. Résultats scientifiques des voyages en Afrique d'Edouard Foà*, 612–702. Imprimerie Nationale, Paris.
- 1909. Recherches sur la malacologie de l'Afrique équatoriale. *Archives de Zoologie Expérimentale et Générale*, Ser. 5, 1: 1–195.
- 1916. Etude sur les mollusques terrestres et fluviatiles recueillis par L. Fea pendant son voyage en Afrique occidentale et aux îles du golfe de Guinée. *Annali del Museo Civico di Storia Naturale, Genova*, Ser. 3, 7: 150–337.
- 1935. Contributions à l'étude de la faune de Mozambique. Voyage de M.P. Lesne (1928–1929). 17^e note – Mollusques terrestres et fluviatiles de la Province de Mozambique (Afrique orientale Portugaise). *Memórias e Estudos Museu Zoológico, Universidade Coimbra*. Ser. 1, 80: 1–72.
- 1936. Contributions à la faune malacologique de l'Afrique équatoriale. LXX. Mollusques terrestres de la Province du Kivu (Afrique orientale). *Bulletin, Muséum National d'Histoire Naturelle, Paris*, Ser. 2, 8: 146–157.
- Haas, F. 1936. Binnen-Mollusken aus Inner-Afrika, hauptsächlich gesammelt von Dr. F. Haas Während der Schomburgk-Expedition in den Jahren 1931–32. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, No. 431.
- International Commission On Zoological Nomenclature. 1985. *International Code of Zoological Nomenclature, Third Edition*. London: International Trust for Zoological Nomenclature.
- Jousseume, F. 1884. Description de mollusques nouveaux. *Bulletin Société Zoologique, France*, 9: 169–192.
- Kilius, R. 1992. Die Typen und Typoide der Mollusken-Sammlung des Zoologischen Museums in Berlin (11). II. Euthyrcura, Stylommatophora, Sigmurethra: Achatinoidea 2, Achatinidae. *Mitteilungen Zoologisches Museum, Berlin*, 68: 157–180.
- Kobelt, W. 1910. Die Molluskenausbeute der Erlangerschen Reise in Nordost-Afrika. Ein Beitrag zur Molluskengographie von Afrika. *Abhandlungen Senckenbergischen Naturforschenden Gesellschaft*, 32: 1–97.
- Lamarck, J.B.P.A. de 1838. *Histoire naturelle des animaux sans vertèbres*, Deuxième édition, 8: 313.
- Martens, E. von 1876. Die von Prof. Dr. R. Buchholz in Westafrika gesammelten Land- und Süßwasser-Mollusken. *Monatsbericht der Königlich Akademie der Wissenschaften zu Berlin* 1876: 253–274.
- 1891. Herrn Preuss bei der Barombi-Station in Kamerun gesammelten Land- und Süßwasser-Mollusken. *Sitzungsberichte Gesellschaft Naturforscher Freund, Berlin*, 1891: 29–34.
- Mead, A.R. 1950. Comparative genital anatomy of some African Achatinidae (Pulmonata). *Bulletin of the Museum of Comparative Zoology at Harvard College*, 105: 219–291.
- 1986. Anatomical studies transfer *Leucotaenius* from Achatinidae to Acaevidae (Pulmonata: Sigmurethra). *Archiv für Molluskenkunde*, 116: 137–155.
- (1992) Anatomical criteria in the systematics of the Achatinidae (Pulmonata). *Proceedings, Tenth International Malacological Congress, Tübingen* 1989.
- Meredith, H.M. 1983a. An introduction to slugs and land snails, with a key to genera of the larger species known to occur in Malawi. *Nyala*, 9: 23–34.
- 1983b. Species and localities of terrestrial Mollusca known to occur in Malawi – a study of the literature 1865–1983. *Achatina*, 12: 242–259.
- Morelet, A. 1860. Description de nouvelles espèces de l'Afrique occidentale, rapportées par M. le capitaine Vignon. *Journal de Conchyliologie*, 8: 189–191.
- 1866. Coquilles nouvelles recueillies par le Dr. Fr. Welwitsch dans l'Afrique équatoriale, et particulièrement dans les provinces portugaises d'Angola et de Benguela. *Journal de Conchyliologie*, 14: 153–163.
- 1868. *Voyage du Dr. Friedrich Welwitsch. Exécuté par ordre du gouvernement portugais dans les royaumes d'Angola et de Benguela. Mollusques terrestres et fluviatiles*. J.B. Baillière et Fils, Paris.
- Oliver, P.G. 1983. The Melvill-Tomlin Collection. Achatinacea (Achatinidae). *Handlists of the Molluscan Collections in the Department of Zoology, National Museum of Wales, Cardiff*. Ser. 1, pt. 17, 24 pp.
- Ortiz de Zarate Lopes, A. & Ortiz de Zarate Rocandio, A. 1959. *Descripcion de los molluscos terrestres de la Isla de Fernando Poo (Familia Achatinidae)*. Instituto de Estudios Africanos; Consejo Superior de Investigaciones Científicas, Madrid.
- Pain, T. & Verdcourt, B. 1962. On the occurrence of *Achatina tavaresiana* Morelet in Tanganyika Territory. *Journal of Conchology*, 25: 82.
- Parkinson, B., Hemmen, J. & Groh, K. 1987. *Tropical land shells of the world*. Hemmen, Wiesbaden.
- Pfeiffer, L. 1856. Descriptions of twenty-five new species of land-shells, from the collection of H. Cumming, Esq. *Proceedings of the Zoological Society of London*, 1856: 32–36.
- 1859. *Monographia Heliceorum Viventium*. 4: 603. F.A. Brockhaus, Lipsiae.
- 1868. *Monographia Heliceorum Viventium*. 6: 216. F.A. Brockhaus, Lipsiae.
- 1877. *Monographia Heliceorum Viventium*. 8: 275. F.A. Brockhaus, Lipsiae.
- Pilsbry, H.A. 1904–05. *Manual of Conchology, Second Series*, 17. Academy of Natural Sciences, Philadelphia.
- 1909. *Manual of Conchology, Second Series*, 20. Academy of Natural Sciences, Philadelphia.
- 1919. A review of the land mollusks of the Belgian Congo chiefly based on the collections of the American Museum Congo Expedition, 1909–1915. *Bulletin, American Museum of Natural History*, 40: 1–370.
- & Cockerell, T.D.A. 1933. African Mollusca, chiefly from the Belgian Congo. *Proceedings of the Zoological Society of London*, 1933: 365–375.
- Preston, H.B. 1909. Descriptions of seventeen new species and varieties of land and freshwater shells from East and West Africa and the Transvaal. *Annals and Magazine of Natural History, London*, Ser. 8, 3: 180–187.
- Putzeys, S. 1898. Diagnoses de quelques coquilles nouvelles provenant de l'état indépendant du Congo. *Annales, Société Royale de Malacologie Belgique*, 27: iv–vi.
- Schacko, G. 1881. Radula-Untersuchungen. pp. 122–127 In: von Martens, E. *Conchologische Mittheilungen als Fortsetzung der Novitates conchologicae*. Cassel. 3(2).
- Schouteden, H. 1935a. Les achatines (Bulletin Cercle Zoologie du Congo). *Revue de Zoologie et de Botanique Africaines*, 26: 110–112.
- 1935b. Quelques mollusques Congolais. *Revue de Zoologie et de Botanique Africaines*, 27: 286–292.
- Smith, E.A. 1881. On a collection of shells from Tanganyika and Nyassa, and other localities in East Africa. *Proceedings, Zoological Society of London*, 1881: 276–300.
- 1890. A list of the species of *Achatina* from South Africa, with the description of a new species. *Annals and Magazine of Natural History, Series 6*, 6: 390–394.
- 1899. On a collection of land-shells from British Central Africa. *Proceedings, Zoological Society of London*, 1899: 579–592.
- Solem, A. 1972. Malacological applications of scanning electron microscopy II. Radular structure and functioning. *Veliger*, 14: 327–336.
- Sowerby, G.B. 1890. Descriptions of thirteen new species of land-shells, with a note on *Bulimus fulminans*. *Proceedings, Zoological Society of London*, 1889: 577–582.
- Spence, G.C. 1928. Non-marine mollusca from West Africa. *Journal of Conchology*, 18: 211–216.
- Thiele, J. 1911. Mollusken der Deutschen Zentralafrika Expedition. *Wissenschaftliche Ergebnisse Deutschen Zentral Afrika Expedition (1907–08)*, 3: 175–212.
- 1929. *Handbuch der Systematischen Weichtierkunde*. Gustav Fischer, Jena.
- U.S. Board On Geographic Names. *Gazetteers*. U.S. Department of Interior. Washington, D.C.
- Vaught, K.D. 1988. *A classification of the living Mollusca*. American Malacologists, Burlington.
- Verdcourt, B. 1966. The identity of *Achatina bloyeti* Bourguignat (Mollusca: Achatinidae) with some notes on other species of the genus occurring in East Africa. *Revue de Zoologie et de Botanique Africaines*, 74: 97–120.
- 1983. A list of the non-marine Mollusca of East Africa (Kenya, Uganda, Tanzania, excluding Lake Malawi). *Achatina*, 11: 200–239.
- Zilch, A. 1959. *Gastropoda von Wilhelm Wenz, Teil 2 Euthyneura*. Gebrüder Borntraeger, Berlin-Nikolassee.